

Climate-crop interactions in the U.S. winter wheat belt

by

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B.S., Heilongjiang Bayi Agricultural University, 2019

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Abstract

Climate change poses severe challenges to global food security. Wheat is one of staple food crops worldwide, and its production faces mounting pressures from rising food demand due to quick increase in world population. Furthermore, increasing exposure to climate extremes, such as heat and drought, during sensitive growth stages can cause abrupt yield shocks, threatening its production sustainability. However, the mechanisms underlying climate-crop interactions remain poorly understood despite decades of research. The U.S. Great Plains is the nation's primary hard winter wheat belt and breadbasket. Recent rapid changes in temperature and precipitation during wheat development have significantly affected wheat production in the region. To address these issues, we investigated how drought shocks, breeding progress, and phenological shifts have collectively shaped winter wheat resilience under historical climate change in the region. By analyzing long-term surface climate data from dryland wheat-growing regions at both county- and site levels using statistical and machine-learning approaches, we showed that the unprecedented 2022-2023 drought reduced U.S. hard winter wheat production by 37% through both yield reduction and crop abandonment, driving Dust Bowl-like impacts. Random forest and game-theoretic analyses revealed that spring drought primarily drove yield reduction, whereas fall drought dominated crop abandonment. Moreover, the La Niña phase of the El Niño-Southern Oscillation (ENSO) significantly increased abandonment rates compared to El Niño, underscoring the need to jointly address yield decline and abandonment to stabilize production under climate extremes. Analyzing cultivar-specific data from 1982 to 2020, we found that compound hot-dry (HD) events during the grain filling period reduced yields by an average of 6%, whereas breeding-driven yield gains were accompanied by reduced HD resilience: newer cultivars exhibited greater yield potential but increased sensitivity to HD stress. These findings revealed a trade-off between

productivity and resilience, pointing to the urgent need to reorient breeding strategies toward increasing abiotic stress tolerance. To investigate the long-term climate trend impacts on yield, we accounted for climate-driven shifts in phenology, often overlooked in previous studies, by tracking the same cultivar cultivated in the same fields across decades. We approximated this experiment using the constant check cultivar ‘Kharkof,’ cultivated for 65 years (1960-2024) across the Great Plains, and demonstrated that long-term warming advanced phenological stages and extended the reproductive window (double ridge-heading), partially offsetting the negative impacts of heat stress. Warming also reduced cold injury in high-latitude regions, contributing to yield gains. In contrast, the fixed-season assumption overestimated the negative impacts of climate trends by nearly threefold, largely because it exaggerated the negative effects of rising temperatures. Those findings highlight the critical role of phenological shifts in modulating climate impacts on crop yields and provide a more nuanced understanding on how historical climate trends have shaped crop yields. This work provides a more nuanced view of climate-crop interactions and identifies adaptation pathways, which may benefit development of climate-informed policy for improvement of wheat breeding strategy and abiotic stress management.

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Chapter 1 - Introduction

Wheat is a major global staple crop, providing about one-fifth of the world's dietary calories and playing a vital role in food security¹. However, wheat production is increasingly challenged by climate variability, extreme weather, and socio-economic disruptions^{2,3}. Recent years have seen the dual pressures of climate extremes, such as drought and heat stress^{4,5}, and geopolitical instability¹, which has disrupted global wheat supply chains. As one of the largest wheat producers and exporters, the U.S. plays a crucial role in stabilizing the global wheat market^{4,5}. Yet, U.S. wheat production has experienced substantial yield losses and crop abandonment due to extreme climate events. Understanding how climate extremes, breeding progress, and long-term climate change affect U.S. winter wheat production is essential for ensuring future food security and guiding adaptation strategies. This dissertation addresses these challenges through three interconnected studies, each focusing on a distinct but complementary aspect of climate impacts on winter wheat.

The first study examines the unprecedented drought during the 2022-2023 growing season, which caused record-low precipitation and severe yield losses across the U.S. winter wheat belt. The drought was particularly severe in Kansas, the nation's leading wheat-producing state⁴, where precipitation dropped 60% below the long-term average, causing poor establishment and compromised yield potential. Using combinatorial analytics and a random forest modeling framework, this chapter quantifies the impacts of extreme drought and other climatic anomalies on both yield and crop abandonment. Additionally, the study explores how large-scale climate phenomena, such as ENSO phases^{6,7}, modulate regional production outcomes. By linking observed yield and abandonment losses to underlying climatic drivers, this chapter provides critical insights

into the mechanisms behind extreme production shocks and underscores the vulnerability of U.S. winter wheat systems to rare but high-impact climatic events.

The second study focuses on the role of historical breeding programs in improving climate resilience, particularly to compound hot-dry events, which severely impact U.S. agriculture^{5,8} and cause global crop yield losses of up to 30%⁹. Climate resilience refers to the capacity of a system to maintain stable performance under varying environmental stress levels, and in wheat, this is reflected by cultivars' ability to sustain yield improvements under stressed environments¹⁰⁻¹². Using field trial data from the U.S. Hard Winter Wheat region, this chapter assesses whether yield gains have been maintained across different environmental stress levels and breeding progress has enhanced cultivar tolerance to hot-dry events. By linking breeding progress with climate sensitivity, the study provides empirical evidence of how the sensitivity of modern cultivars to hot-dry events has changed over time and offers guidance for breeding programs aimed at enhancing resilience to climatic stresses. This analysis not only informs breeding priorities but also provides insight into the broader interactions between genetic improvement and environmental pressures.

The third study investigates how long-term climate change and phenological shifts influence winter wheat yield trends across the Great Plains. Crop development is strongly temperature-dependent, and warming conditions accelerate growth, advancing key stages such as heading and flowering¹³⁻¹⁷. These shifts can either exacerbate or mitigate exposure to climatic stresses, depending on the timing of heat, drought, or frost events. Most previous studies assume a fixed growing season¹⁸⁻²¹, potentially overlooking the effects of phenological adaptation. By isolating the effects of phenological adaptation from those of direct climate forcing, this study provides a more realistic assessment of how gradual warming and changing precipitation patterns have shaped winter wheat yield trends over time. Using a long-term fixed-cultivar dataset from the

U.S. Hard Winter Wheat Regional Nursery Program, the study quantifies climate-driven yield changes while controlling for genetic effects. This work advances understanding of long-term climate impacts and informs future adaptation and management strategies.

References

1. Shiferaw, B., Smale, M., Braun, H. J., Duveiller, E., Reynolds, M., & Muricho, G. (2013). Crops that feed the world 10. Past successes and future challenges to the role played by wheat in global food security. *Food Secur.*, 5(3), 291-317.
2. F. Lin, X. Li, N. Jia, F. Feng, H. Huang, J. Huang, S. Fan, P. Ciaais, X.-P. Song, The impact of Russia-Ukraine conflict on global food security. *Glob. Food Sec.* **36**, 100661 (2023).
3. Bentley, A. R. *et al.* Near-to long-term measures to stabilize global wheat supplies and food security. *Nat. Food* **3**, 483-486 (2022).
4. Tack, J., Barkley, A. & Nalley, L. L. Effect of warming temperatures on US wheat yields. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 6931-6936 (2015).
5. Zhao, H. *et al.* US winter wheat yield loss attributed to compound hot-dry-windy events. *Nat. Commun.* **13**, 1-9 (2022).
6. S. D. Schubert, M. J. Suarez, P. J. Pegion, R. D. Koster, J. T. Bacmeister, Causes of long-term drought in the US Great Plains. *J. Clim.* **17**, 485-503 (2004).
7. K. C. Mo, Interdecadal modulation of the impact of ENSO on precipitation and temperature over the United States. *J. Clim.* **23**, 3639-3656 (2010).
8. Mittler, R. Abiotic stress, the field environment and stress combination. *Trends Plant Sci.* **11**, 15-19 (2006).
9. Lesk, C. *et al.* Compound heat and moisture extreme impacts on global crop yields under climate change. *Nat. Rev. Earth Environ.* **3**, 872-889 (2022).
10. Bailey-Serres, J., Parker, J. E., Ainsworth, E. A., Oldroyd, G. E. & Schroeder, J. I. Genetic strategies for improving crop yields. *Nature* **575**, 109-118 (2019).
11. Langridge, P., Braun, H., Hulke, B., Ober, E. & Prasanna, B. Breeding crops for climate resilience. *Theor. Appl. Genet.* **134**, 1607-1611 (2021).
12. Ober, E. S. *et al.* Wheat root systems as a breeding target for climate resilience. *Theor. Appl. Genet.* **134**, 1645-1662 (2021).
13. Hu, Q., Weiss, A., Feng, S. & Baenziger, P. S. Earlier winter wheat heading dates and warmer spring in the US Great Plains. *Agric. For. Meteorol.* **135**, 284-290 (2005).
14. Chmielewski, F.-M., Müller, A. & Bruns, E. Climate changes and trends in phenology of fruit trees and field crops in Germany, 1961–2000. *Agric. For. Meteorol.* **121**, 69-78 (2004).
15. Menzel, A. *et al.* European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* **12**, 1969-1976 (2006).
16. Estrella, N., Sparks, T. H. & Menzel, A. Trends and temperature response in the phenology of crops in Germany. *Glob. Change Biol.* **13**, 1737-1747 (2007).
17. Fatima, Z. *et al.* The fingerprints of climate warming on cereal crops phenology and adaptation options. *Sci. Rep.* **10**, 18013 (2020).

18. Moore, F. C. & Lobell, D. B. The fingerprint of climate trends on European crop yields. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 2670-2675 (2015).
19. Kukal, M. S. & Irmak, S. Climate-driven crop yield and yield variability and climate change impacts on the US Great Plains agricultural production. *Sci. Rep.* **8**, 1-18 (2018).
20. Lobell, D. B., Schlenker, W. & Costa-Roberts, J. Climate trends and global crop production since 1980. *Science* **333**, 616-620 (2011).
21. Wang, Z., Ye, T., Wang, J., Cheng, Z. & Shi, P. Contribution of climatic and technological factors to crop yield: empirical evidence from late paddy rice in Hunan Province, China. *Stoch. Environ. Res. Risk Assess.* **30**, 2019-2030 (2016).

Chapter 2 - An unprecedented fall drought drives Dust-Bowl-like losses associated with La Niña events in U.S. wheat production

2.1 Introduction

Global wheat production faces a challenge due to the ongoing conflict between Ukraine and Russia, which has resulted in a 60% reduction in wheat trade and, consequentially, a 50% surge in wheat prices^{1,2}. In response to this crisis, the U.S., which is recognized as the “wheat breadbasket of the world,” expanded its acreage of winter wheat by 11% during 2022/2023 compared to the previous year. During this period, the U.S. wheat heartland encountered an unforeseen and unprecedented challenge from extreme weather events. In the fall of 2022 (August - October), most states in the U.S. winter wheat belt, including Texas, Oklahoma, Kansas, Colorado, and Nebraska, experienced a substantial precipitation deficit (Figure 2.1a). This drought was particularly detrimental in Kansas, known as the “wheat state,” which produces the most winter wheat in the U.S.³. In the past 40 years (1981-2020), Kansas produced 359 million bushels of winter wheat per year on average, representing 23% of the U.S. total. In 2022/2023, Kansas had a record-setting precipitation deficit dating back to 1896 (Figure 2.1a,b), with the amount of precipitation falling to 84 mm, 60% below the average between 1981-2010. Similar precipitation patterns and dryness rankings were observed across the entire U.S. winter wheat belt (Figure 2.1a).

Such an extreme drought affected winter wheat emergence, growth, and development, leading to the latest emergence date and the second-longest duration between planting and emergence dates in the past 40 years, which covers all available historical data (Figure 2.1c). These adverse conditions dually compromised both establishment and growth. Furthermore, crop growth conditions in the first week of November 2022 were the poorest on record over the period from

1987 to 2023 (Figure 2.1d). The severe drought conditions persisted into the spring of 2023 (Figure 2.1a,b,d), further hampering growth and tillering. In Kansas, the extreme lack of precipitation in

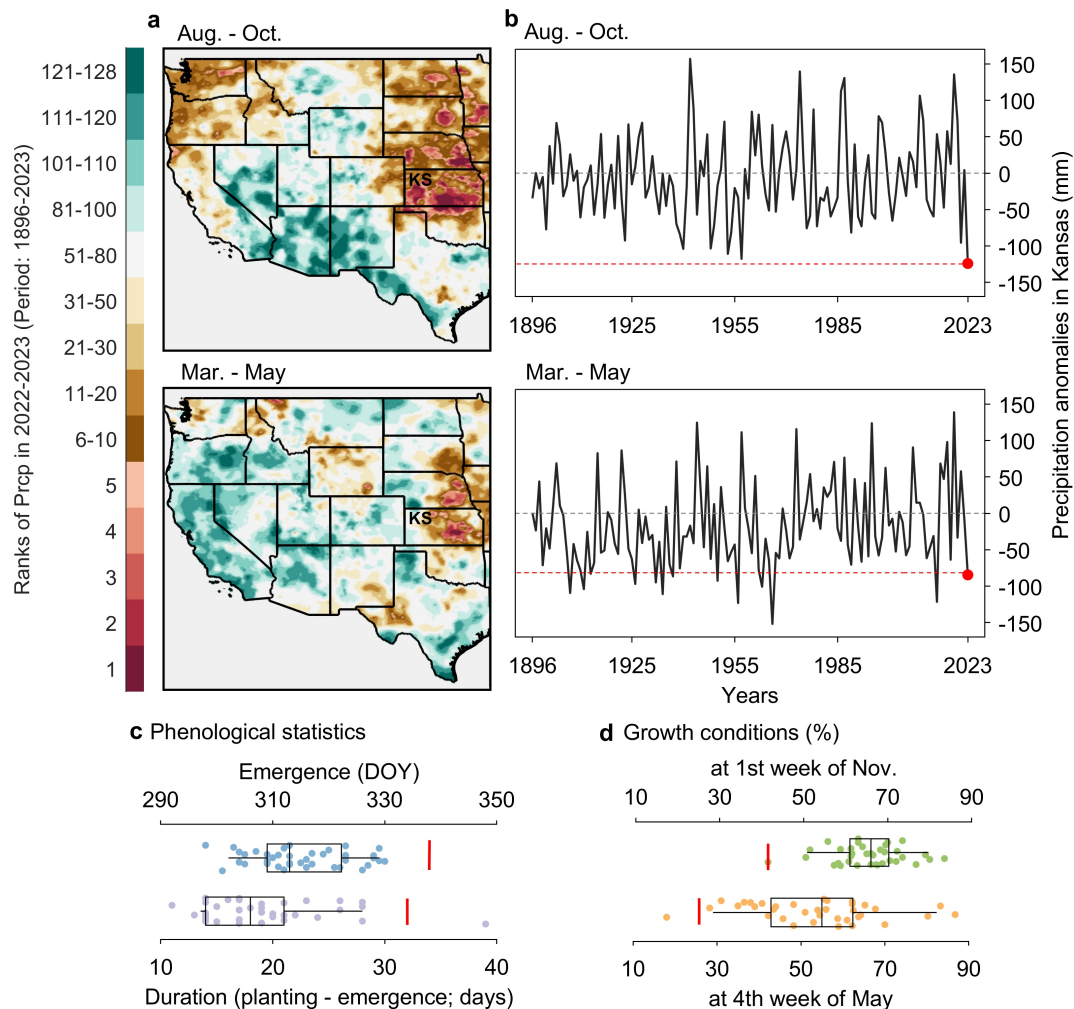


Figure 2.1. Driest rankings in the U.S. over 128 years and the 2022-2023 winter wheat growth conditions in “wheat state” of Kansas (KS). a, Rankings (driest) of accumulated precipitation (Prp) during August-October 2022 and March-May 2023 over the past 128 years (1896-2023; harvested years). b, Precipitation anomalies during August-October and March-May with the base period of 1981-2010 in Kansas. c, Wheat phenological statistics of emergence date (day of year, DOY) and duration between planting and emergence dates (days) from 1982 to 2023. d, Wheat growth conditions (%) in early November (first week) and late May (fourth week) from 1987 to 2023. The boxes delimit the 25th and 75th percentiles; whiskers indicate 5th and 95th percentiles; and vertical black lines represent the 50th percentile. Red solid circles in b and vertical lines in c and d are for 2023 harvest year.

the fall and spring resulted in large portions of winter wheat emerging in late spring rather than in early fall, shortening the period of crop development and compromising the crop’s yield potential.

Using combinatorial analytics, the extreme climatic conditions encountered during the 2022/2023 growing season presented a unique opportunity to understand how such events converge to influence winter wheat production.

Despite increasing research efforts, the quantitative linkages between extreme climatic change and wheat production remain ambiguous. Annual wheat production equals the product of per-harvested-acre yields and harvested acreage⁴. Both production components can theoretically be affected by climate variability and climate change. Most studies have focused on how in-season climatic factors, such as overall growing-season warming^{3,5}, extreme in-season temperatures^{6,7}, and crop-seasonal droughts^{8,9}, affect wheat yields. However, these studies may bear uncertain implications for estimating production variability, because the far-reaching impact of climate extends beyond in-season effects and also beyond mere reductions in crop yields^{8,10-12}. Specifically, crop abandonment, defined as the difference between planted and harvested area normalized to the planted area¹³, contributes to market volatility¹⁴, global food insecurity¹⁵, and greater crop insurance claims, which have been overlooked in many studies^{9,16}. Recent studies have explored the relationship between climate variability and crop abandonment, the results of which are typified by crop failure¹⁰, a decrease in harvested ratio (the ratio of harvested area to planted area)^{17,18}, and changes in crop frequencies (number of crops harvested per growing season)¹⁹. For example, normal temperatures or precipitation tend to increase the harvested ratio, while extreme climate conditions cause it to decrease, particularly in maize and soybean¹⁸. Consequently, relying solely on per-harvested-acre wheat yield as a gauge of production variability can cause uncertainty when estimating the impact of climatic variability on wheat production. To bolster global food security²⁰, it is imperative to integrate crop abandonment data into that of wheat yields when assessing production declines that are attributable to extreme weather events and

climatic changes.

The occurrence of an unprecedented drought in Kansas during the 2022/2023 pre-season and growing season, along with the availability of long-term data on wheat production in the state dating back to 1926, allowed us to explore the underlying mechanistic impacts of extreme climatic events on variability of wheat production. Utilizing a random forest (RF) regression model²¹, we provide quantitative evidence of 2023 production loss resulting from both crop abandonment and yield variation, and compared that to the winter wheat production loss in both the decade of the Dust Bowl (*i.e.*, 1930s), which was marked by the most prolonged and severe drought in modern U.S. history^{22,23}, and the latest decade between 2013-2022. We then quantitatively disentangled the climatic drivers underlying the extreme events that caused the extreme crop abandonment and yield losses by integrating the RF model with a game theory tool²⁴. Our objectives were to understand the impact of pre-seasonal and in-season droughts on winter wheat production including crop abandonment and yield losses *per se*. Considering the widespread influence of the El Niño Southern Oscillation (ENSO) on fall precipitation in the U.S. winter wheat belt^{25,26} and high predictability of larger amplitude ENSO events^{27,28}, we simultaneously explored the potential connections between ENSO phases and crop abandonment that might benefit predictive crop monitoring and early warning systems²⁹ in the U.S. winter wheat belt.

2.2. Material and Methods

2.2.1 Data

County- and state-level winter wheat yield, harvested area, and planted area data were retrieved from the U.S. Department of Agriculture, National Agricultural Statistics Service (USDA-NASS) for all counties in Kansas and spanning the years 1926-2023. State-level planting

and emergence dates (1982-2023) and weekly crop condition reports (1987-2023) were also collected from USDA-NASS, which are the longest length available for the data. Climatic data (precipitation, maximum temperature, and minimum temperature) from 1895 to 2023 were obtained from the monthly U.S. Historical Climatology Network (USHCN) maintained by the National Oceanic and Atmospheric Administration (NOAA). The monthly sea surface temperatures (SST) were taken from the Met Office Harley Centre Observations datasets (HadISST v1.1)³⁰ for calculating ENSO signals based on the Niño3.4 region (5°N – 5°S, 120° – 170°W). Crop conditions were evaluated using an index ranging from 0 to 100%³¹. The growing season of winter wheat is generally considered to be September-May in Kansas⁷, but we used climatic data starting in August to capture the effects of climate in the month preceding planting. We divided the growing season into fall (August-October), winter (November-February), spring (March-April), and early summer (May, wheat grain filling).

2.2.2 Modelling

Based on the conceptual framework (Supplementary Text A), we ran two separate random forest (RF) models to estimate two components of production losses due to climate variation: the abandonment fraction and yield anomalies. Abandonment fraction here is expressed as $\frac{PA-HA}{PA}$, where PA and HA are the planted and harvested areas, respectively, in hectares. This expression enables meaningful comparisons across different county-years with varying planted areas. Yield anomalies were calculated as the difference between actual yields and expected yields, with expected yields representing the historical yield trends driven by agricultural advancements in breeding technology and crop management. Thus, a negative anomaly suggests that yields are less than expected, possibly due to an adverse climate, disease, or other challenges. Yield trends were

evaluated using a locally weighted smoothing regression³² with the standard setting of the function (Figure A.10).

The RF specifications for abandonment fraction (*fab*) and yield anomaly (ΔY) are:

$$fab_{c,y} = F(clm_{c,y}, price_y) + \varepsilon_{c,y} \quad [1]$$

$$\Delta Y_{c,y} = F(clm_{c,y}) + \varepsilon_{c,y} \quad [2]$$

where F is a random forest function; $clm_{c,y}$ represents the climate variables including monthly or seasonal maximum temperature (T_x , °C) and minimum temperature (T_n , °C), and accumulated precipitation (Pr_{cp} , mm) during four growth periods for county “ c ” and year “ y ”; the detrended $price_y$ (inflation-adjusted based on the consumer price index of 2023) by the locally weighted smoothing regression was incorporated into the “*fab*” model to isolate the effects of price changes on farmers’ decisions to abandon their crop; $\varepsilon_{c,y}$ refers to the error. The number of trees and the number of variables tested at each node in the RF model are two key parameters²¹. In order to determine the optimum parameters for each model above, we partitioned 90% of data to train model and remaining 10% of data to test model. The model predicted performance was estimated by the coefficient of determination (R^2) and root mean square error (RMSE) (Table A.1 and Figure A.1).

The RF results were used to estimate climate-driven production changes from yield and abandonment relative to the historical climate-driven average production over 1981-2010 ($\widehat{P_{base}}$) for the Dust Bowl decade (1931-1940), the latest decade (2013-2022), and year 2023. The wheat price in the “*fab*” model was fixed to the average of 1981-2010 to isolate price effects. State-level production change ($\%P'$) in specific years of interest (e.g., 2023) was defined as a relative change:

$$\%P'_y = \frac{\Delta P_{fab,y} + \Delta P_{Y,y}}{\widehat{P_{base}}} \times 100 \quad [3]$$

where $\Delta P_{fab,y}$ and $\Delta P_{Y,y}$ are defined as climate-caused production changes from the changes in

abandonment and in yields, respectively. Details of calculations for these two components are given in Supplementary Text A.

2.2.3 The climate driver of extreme abandonment or yield loss

Next, we integrated a game theory (Shapley additive explanations, SHAP)²⁴ into the RF models (Eqs. [1] and [2]) to assess the critical climate drivers in extreme wheat abandonment and yield loss. Specifically, for all instances of extreme wheat abandonment and yield loss events, we used SHAP values to infer variable importance in the model outcome³³. SHAP values are a machine learning analogue of partial regression, quantifying the relative importance of each variable on the outcome while considering all other variables in the model. The overall variable importance was determined by the mean of the absolute value of the SHAP values, and the marginal effect of variable with the highest relative importance was visualized by plotting the covariate versus the corresponding SHAP value for each observation. Finally, we assessed the critical extreme climate drivers in severe wheat abandonment and yield losses (Supplementary Text A).

2.2.4 Robustness checks

To ensure the robustness of our analysis, we conducted two checks on the RF models with two additional sets of predictors. First, we substituted the precipitation in our preferred RF models with the mean monthly Palmer Z-index sourced from NOAA. The Z-index is a measure of the monthly moisture anomaly and reflects the departure of moisture conditions from normal moisture conditions in a particular month³⁴. Second, due to the high collinearity between mean temperature and extreme hot/cold days, we tested the fraction of warm days and cold days to replace the mean

T_x and T_n in our models to evaluate our results (Figures A.4 and A.5, and Table A.1). Specifically, the daily maximum and minimum temperatures were taken from the daily Global Historical Climatology Network (GHCN) and interpolated with a Delaunay Triangulation method³⁵ to the centroid of each county in Kansas. Then, we defined the fraction of warm/cold days by calculating the number of days with maximum/minimum temperatures above/below the local historical 90th/10th percentile divided by the duration of growing season.

2.2.5 Crop abandonment statistics during ENSO phases

To spatially analyze the impacts of ENSO oscillation on crop abandonment, we broadened our coverage to encompass the entire U.S. winter wheat belt, including Nebraska, Colorado, Kansas, Oklahoma, and Texas. Data for planted and harvested areas at the county and state levels were collected from USDA-NASS, and corresponding available years are provided in Table A.2. We selected counties with both more than 50 available years of data and an average harvested area (1981-2010) exceeding 5,000 hectares. We next calculated averages of detrended crop abandonment (*fab*) based on locally weighted smoothing regression (i.e., Figure A.11) at specific ENSO phases:

$$\begin{aligned} fab_{El\ Ni\tilde{no},c} &= \frac{\sum_{y=initial}^{2023} fab'_{c,y}}{N_{El\ Ni\tilde{no}}}; & ENSO > 0.5 \\ fab_{La\ Ni\tilde{na},c} &= \frac{\sum_{y=initial}^{2023} fab'_{c,y}}{N_{La\ Ni\tilde{na}}}; & ENSO < -0.5 \end{aligned} \quad [4]$$

where $fab_{El\ Ni\tilde{no},c}$ and $fab_{La\ Ni\tilde{na},c}$ are the average crop abandonment anomalies in El Niño and La Niña years (“y”) for county “c”, respectively; *N* refers to year numbers of the specific ENSO phase; *fab'* refers to detrended crop abandonment anomalies. The ENSO signal here is defined as a 3-month running mean after being linearly detrended and standardized. We specifically

calculated the average ENSO signals for Texas and Oklahoma from December to February, and for Kansas, Colorado, and Nebraska from August to October. These selected periods align with the planting dates of winter wheat⁷. Based on the same method, the state-level $fab_{El\ Ni\tilde{no}}$ and $fab_{La\ Ni\tilde{na}}$ were also calculated. We then calculated the difference of fab anomalies between La Niña and El Niño phases as,

$$\Delta fab_c = fab_{La\ Ni\tilde{na},c} - fab_{El\ Ni\tilde{no},c} \quad [5]$$

Positive (or negative) values of Δfab indicate that the La Niña phase exacerbates (or mitigates) crop abandonment relative to the El Niño phase. The statistical significance for changes in Δfab_c were determined through a bootstrapping sampling procedure ($n = 10,000$) at a 95% confidence level. The mean change for each bootstrap sample was calculated, and the change was considered statistically significant if, in a two-sided t test, over 97.5% of the sample means were consistently smaller or larger than zero.

2.3. Results and Discussion

2.3.1 Attributions of losses in winter wheat production

The observational data revealed that abandonment of winter wheat was the most severe during the 2022/2023 growing season in Kansas since the Dust Bowl era in 1930s, the exception being the year of 1951 (Figure 2.2a), with an abandonment of 29%, amounting to 951,011 hectares. This severity of abandonment mirrors that of the broader U.S. winter wheat belt, in which 2022/2023 recorded the highest level of abandonment since the middle of the Dust Bowl period (Figure 2.2a). Such pronounced abandonment can be attributed to delayed emergence, adverse crop developmental conditions (Figure 2.1c,d), and diminished yield prospects. These unfavorable outcomes ultimately compelled farmers to leave their crops unharvested. Similarly, we also found

a large yield loss in Kansas (Figure 2.2a), with a decrease of 0.52 t ha^{-1} compared to the expected yield, equivalent to 22% of expected yield (see Methods).

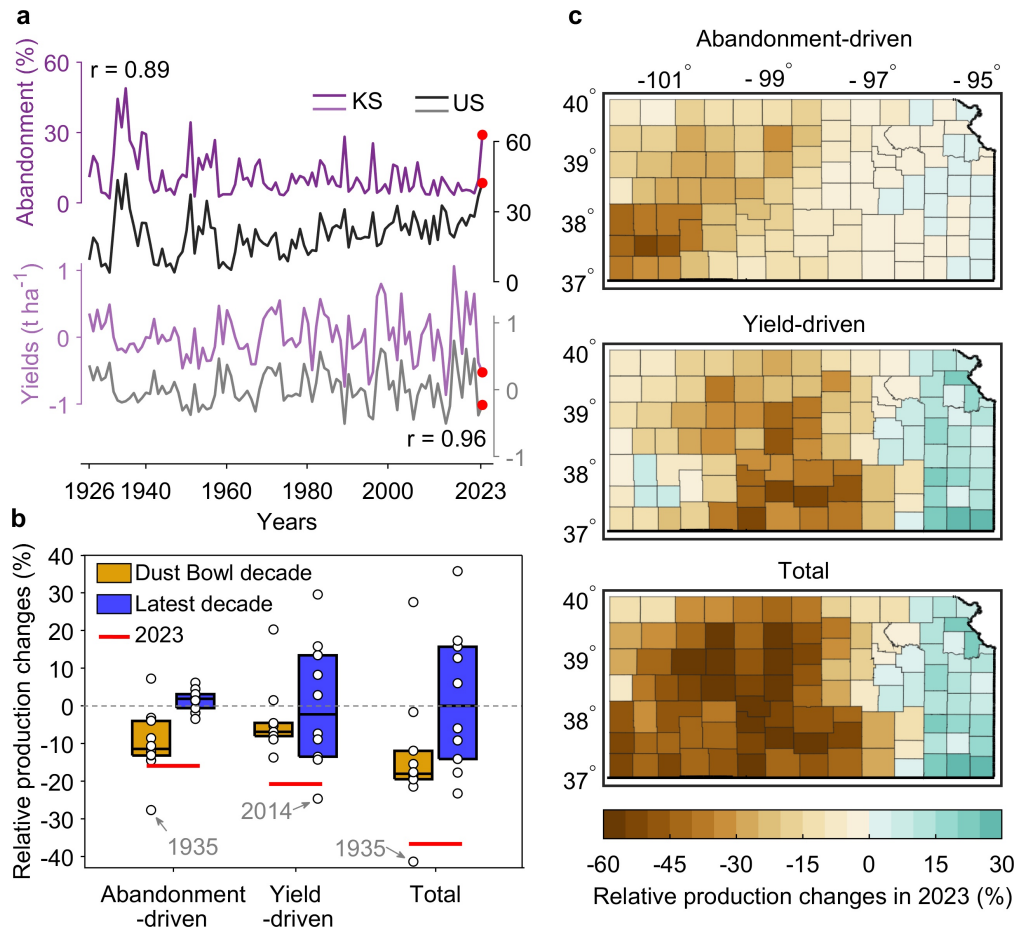


Figure 2.2. Climate-driven changes in production attributed to crop abandonment and yields. a, Observed time series for both crop abandonment and yield anomalies for Kansas (KS) and the U.S. winter wheat belt (US) including Nebraska, Colorado, Kansas, Oklahoma, and Texas. b, State-level relative climate-driven production changes due to changes in abandonment and yields during the Dust Bowl decade (1931-1940), latest decade (2013-2022), and year 2023. The relative production changes are expressed as production changes relative to average production during 1981-2010. The boxes delimit the 25th and 75th percentiles and the horizontal black lines represent the 50th percentile. c, County-level relative production changes due to changes in abandonment and yield in the year 2023.

To quantify the impact of extreme climate during the 2022/2023 growing season on changes in abandonment and yields, we employed a RF regression model. This model captured pre-seasonal and in-season temperature and precipitation variations, as well as wheat price fluctuations (see Methods and Figure A.1). We then assessed the severity of wheat production

losses in the 2022/2023 growing season by comparing them with those during both the decade of the U.S. Dust Bowl (1931-1940) and the most recent decade (2013-2022). All results were expressed as a percentage relative to the estimated average production driven by historical climate records (1981-2010). We found that climatic extremes during 2022/2023 resulted in a 37% loss in wheat production compared to average production during the period of 1981-2010. This loss was the greatest for any year throughout the most recent decade, as well as that of the Dust Bowl era, with the sole exception of 1935 (Figure A.2b). The 2023 production losses were not merely due to yield decline *per se*, contributing to a 21% wheat production loss, but also to crop abandonment (Figure 2.2b). The 16% production losses from crop abandonment in 2022/2023 is noteworthy because they are comparable to the losses caused by extreme drought during the Dust Bowl era. During that historical period, three-quarters of the average production loss of 14% was attributed to crop abandonment, while the remainder (one-quarter) was due to yield reductions *per se* (Figure 2.2b). The role of crop abandonment in influencing crop production was also underscored in maize and soybean¹⁸. Generally, crop abandonment showed a nonlinear response to temperature and precipitation. However, crop abandonment in maize and soybean is more sensitive to temperature¹⁸, whereas wheat abandonment displays greater sensitivity to precipitation (Figure A.2). To provide perspective, during the decade of the Dust Bowl, production losses due to changes in abandonment were much larger than losses resulting from changes in yield. In contrast, during the most recent decade, production losses caused by changes in yield were larger than those caused by changes in abandonment (Figure 2.2b). Additionally, we showed the comparison of observed and estimated abandonment, which augmented the credibility of our findings (Figure A.3). To test the robustness of the findings, we also used two alternative models with different sets of predictors (Figures A.4a and A.5a). Finally, we showed the spatial distribution of climate-driven production

changes in 2023, attributable to changes in crop abandonment and per-harvested-acre yields (Figure 2.2c). The southwest regions of Kansas exhibited the substantial production loss attributed to crop abandonment, whereas the central regions experienced severe decline in production due to yield loss (Figure 2.2c), aligning with regions affected by severe spring drought (Figure 2.1a). Overall, both crop abandonment and yield loss contributed to an average production decline of 50% across the central and western regions (Figure 2.2c). A recent study¹⁷ found that, on average, the projected future climate change by mid-century (2034-2065) does not significantly increase production loss through crop abandonment relative to historical averaged climate. Consequently, it was suggested that neglecting crop abandonment as a factor in future production levels would not substantially influence estimation of climate-driven production losses. However, the calibration period used in this study was relatively short and did not include most of the notable droughts of the past. Given the crucial role of crop production variability in maintaining food stability⁸ and the impact of crop abandonment on production loss (Figure 2.2b,c), we encourage consideration of crop abandonment when estimating impact of climate variability on crop production, especially during extreme drought years. This additional measure could aid policy makers in devising effective risk management strategies and adaptation interventions.

2.3.2 Drivers for extreme abandonment and yield loss

We subsequently disentangled the underlying deleterious climatic conditions that led to both extreme wheat abandonment and the extreme yield loss, defined as events above the 90th percentile and below the 10th percentile, respectively, across all years (1926 to 2023) for each of the 105 counties in Kansas. The 10th and 90th percentiles were also selected for determining climatic extremes, including low and high precipitation, as well as cold and warm temperature

events. When we embedded a game theory tool (Shapley additive explanations, SHAP)²⁴ into the RF regression model (Methods and Supplementary Text A), our results illustrated that pre-seasonal fall precipitation (August-October) was the most important climate variable in relation to the extreme wheat abandonment globally, whereas spring precipitation (March-April) played a pivotal role in the extreme yield loss (Figure 2.3a,b). Specifically, abandonment rates exhibited a nonlinear response to fall precipitation, especially with deficits in fall precipitation correlating to higher abandonment rates (Figure 2.3c). Conversely, spring precipitation deficits were associated with the occurrence of extreme yield loss (Figure 2.3c). Finally, we estimated the primary climate extreme driving severe abandonment and yield loss (Figure A.6 and Supplementary Text A). We found that climatic extremes were the primary factors in 75% and 74% of the areas that suffered severe abandonment and yield loss across Kansas from 1926 to 2023, respectively (Figure 2.3e,f). Additionally, extremely low wheat prices (<10th percentile) accounted for 6.6% of the areas that experienced severe abandonment (Figure A.6). We also found that drought in March-April was the primary factor in 19% of the areas of extreme yield losses (Figure 2.3f). In contrast, abandonment was predominantly triggered by fall drought events, which contributed 24% to the severe abandonment area (Figure 2.3e). Moreover, the excessive precipitation in May was associated with both extreme abandonment and yield loss, which is consistent with another study estimating climate-driven crop failure in the U.S.¹⁰. These results were consistent with those based on two alternative models (Figures A.4b,c, and A.5b,c). Indeed, the role of spring and early summer drought, which is critical for grain filling and yield formulation, has been extensively studied^{3,36}. We also found that droughts in the fall and winter largely contributed to extreme yield losses (Figure 2.3f), consistent with another study³⁷. To our knowledge, however, the significance of fall drought as a catalyst for crop abandonment and subsequent production losses has not

previously been highlighted. The impact of fall drought on wheat abandonment can be attributed to the fact that winter wheat is usually sown in autumn, relying on sufficient soil moisture during this period to establish seedlings with robust root systems that promote healthy growth. Our study substantiates the relationship between fall precipitation, and both observed abandonment rates (Figure A.7) and crop growing conditions at the end of the fall season (Figure A.8).

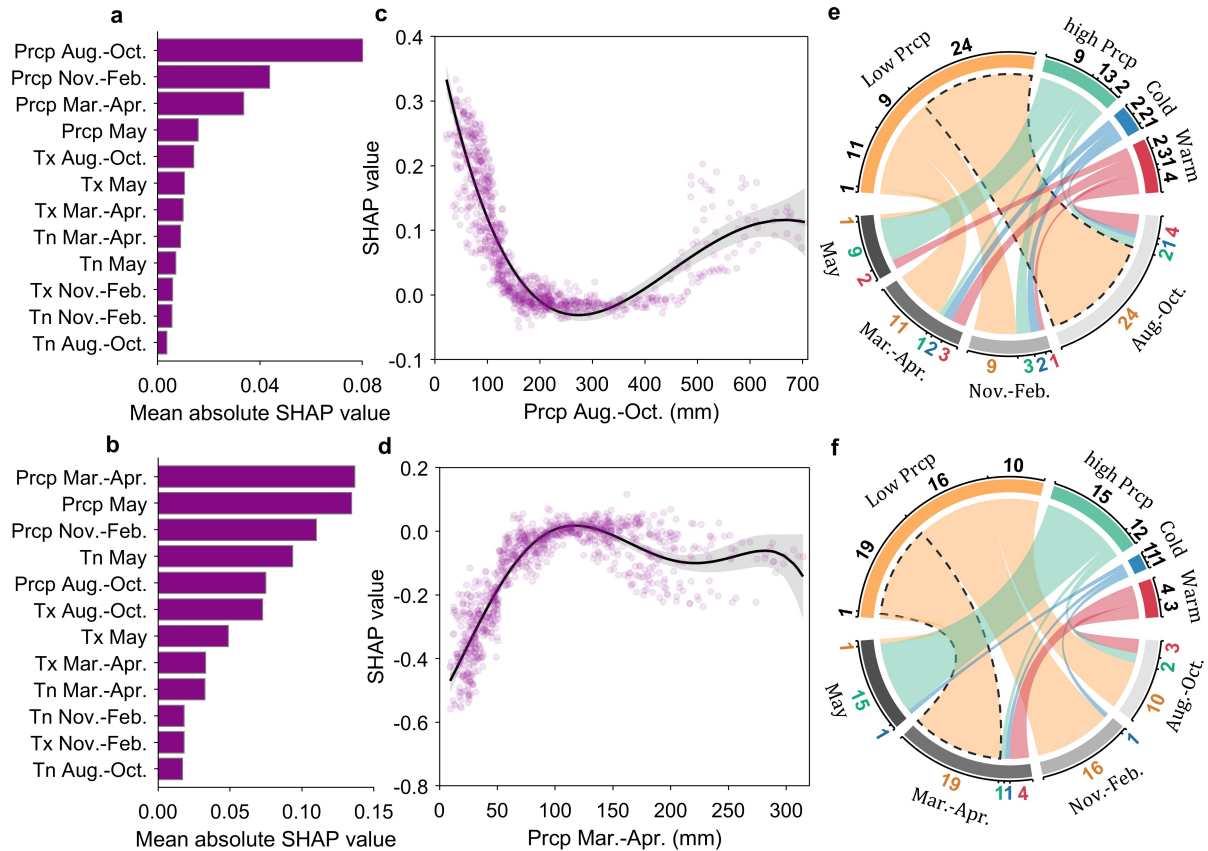


Figure 2.3. Climate drivers of extreme abandonment and extreme yield losses. a, Importance (Shapley additive explanations (SHAP) values) of climate variables during county-years of extreme abandonment ordered from greatest to least important. b, Same as a but during county-years of extreme yield losses. c, Influence of the precipitation (Prcp) during August-October (the most important variable on extreme abandonment). Circles are sample points for county-years of extreme abandonment. Black solid line is fitted line, and shaded area around the solid line indicates 95% confidence interval. d, Same as c but for influence of the precipitation during March-April (the most important variable on extreme yield losses). e, The width (or numbers) of the chords indicates the fractions (%) of area that suffered extreme abandonment (total 75%) driven by primary climatic extremes (low and high precipitation, and cold and warm temperatures) across Kansas from 1926 to 2023. Black dashed lines highlight the most primary climatic drivers. f, Same as e but for fraction of area that suffered extreme yield losses (total 74%).

2.3.3 ENSO teleconnections on winter wheat abandonment

Droughts in the U.S. winter wheat belt have been confirmed to be influenced by the ENSO^{25,38,39}. During La Niña, which is characterized by cooler-than-normal sea surface temperatures in the eastern tropical Pacific, the U.S. winter wheat belt tends to experience fall droughts (Figure A.9), as was observed in the 1930s²⁶, potentially leading to crop abandonment. To explore the direct role of ENSO in explaining variations in crop abandonment, we calculated average anomalies of crop abandonment during both El Niño and La Niña phases (see Methods)^{40,41}. The statistical significance of the changes was determined by bootstrapping ($n = 10,000$) at a 95% confidence level. We found that crop abandonment was reduced during the El

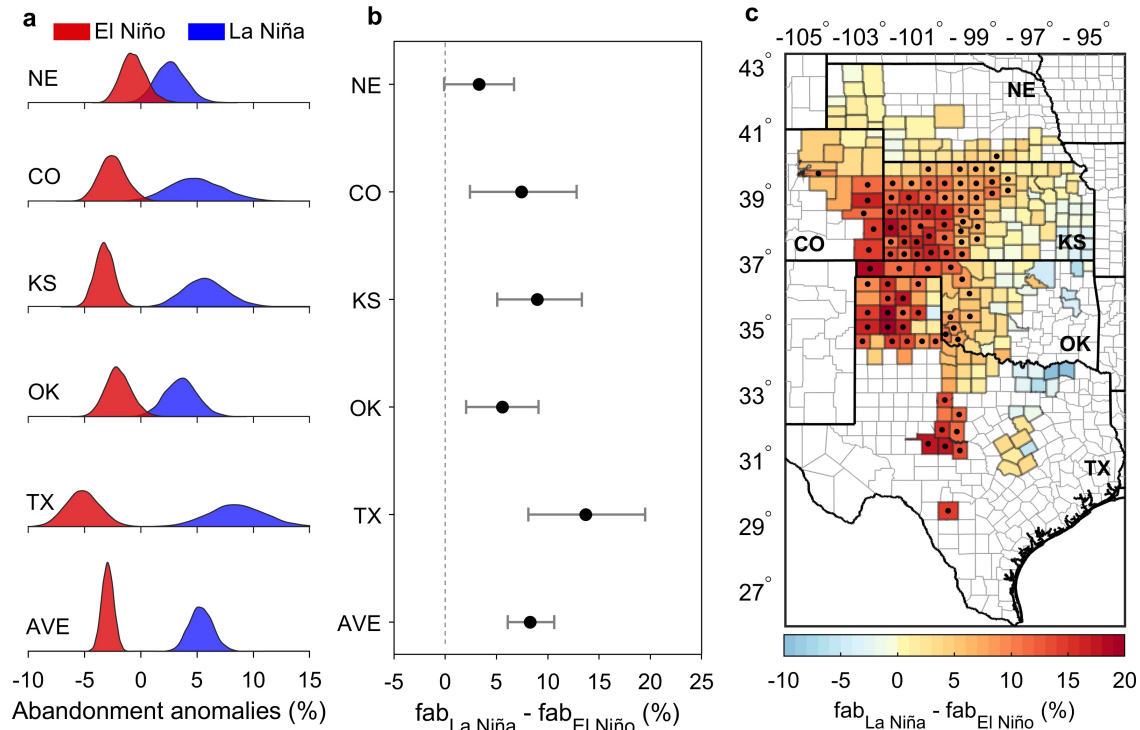


Figure 2.4. Impacts of ENSO phases on crop abandonment anomalies. a, Distributions of state-level crop abandonment (fab) anomalies during El Niño (red) and La Niña (blue) phases in Nebraska (NE), Colorado (CO), Kansas (KS), Oklahoma (OK), and Texas (TX). Negative and positive values indicate ENSO phases decreased and increased crop abandonment, respectively. b, Changes in fab during the transition from El Niño to La Niña phase. Black solid circles indicate averages, and error bars represent 2.5th and 97.5th percentiles. c, County-level changes in crop abandonment between La Niña and El Niño phases. Black dots indicate statistically significant at a 95% confidence level. Note that the state-level impact of ENSO phase on crop abandonment was estimated by using state-level data.

Niño phase across five winter wheat production states, with a significant decrease of 3% on average, ranging from 0.6% to 5.2% (Figure 2.4a). This is expected because El Niño causes the jet stream to shift southward and extend eastward over southern U.S. Conversely, during the La Niña phase, crop abandonment showed a notable increase of 5%, with ranges between 2.7% and 8.6% across states (Figure 2.4a). Except for Nebraska, all states exhibited a notable increase in crop abandonment during the transition from El Niño to La Niña phase, with variations observed among states (Figure 2.4b). In Kansas, the transition from El Niño to La Niña phase intensified crop abandonment by 9%, equivalent to the U.S.-level (Figure 2.4b). We further explored the impacts of ENSO on crop abandonment at a county level across the U.S. winter wheat belt and found that the La Niña phase significantly increased abandonment rates compared to the El Niño phase. The main regions affected by abandonment were in western Kansas, the panhandle areas of Oklahoma, and western Texas (Figure 2.4c), which mirrored the footprint of Dust Bowl-affected regions in the 1930s^{7,23}.

Several studies have suggested the urgent need for a twofold increase in global crop production by 2050 in response to the growing population⁴². Whether or not we are on track to double production by 2050 depends upon sustainable and improved harvestable crop yields^{43,44}. Future production variability in projected climatic scenarios will be influenced by the often-overlooked changes in crop abandonment (Figure 2.2), an especially noteworthy risk given the threats of climatic extremes^{45,46}.

2.4. Conclusion

In summary, our analyses revealed climatic drivers underlying crop abandonment and the influence of ENSO dynamics on winter wheat production. La Niña events increased the probability

of drought events before planting (pre-season) of winter wheat in the U.S. Great Plains. The extremely dry climate in 2022-2023 that followed nearly three consecutive years of La Niña events provided an opportunity to determine the underlying drivers of climatic extremes that negatively impact wheat production. Our study emphasized both the overlooked role of crop abandonment on wheat production in the U.S. winter wheat belt and the underlying climate extremes that drive the two components of production loss—abandonment and yield loss. Recognizing that pre-season droughts primarily drive crop abandonment, farmers could adapt their strategies, such as adjusting planting schedules, selecting drought-resistant cultivars, or investing in water management strategies tailored for the pre-season. These measures can mitigate the effects of these droughts and stabilize crop production. It is also important for policy makers to design and promote initiatives encouraging drought mitigation practices for stable food production.

References

1. F. Lin, X. Li, N. Jia, F. Feng, H. Huang, J. Huang, S. Fan, P. Ciais, X.-P. Song, The impact of Russia-Ukraine conflict on global food security. *Glob. Food Sec.* **36**, 100661 (2023).
2. K. A. Mottaleb, G. Kruseman, S. Snapp, Potential impacts of Ukraine-Russia armed conflict on global wheat food security: A quantitative exploration. *Glob. Food Sec.* **35**, 100659 (2022).
3. J. Tack, A. Barkley, L. L. Nalley, Effect of warming temperatures on US wheat yields. *Proc. Natl. Acad. Sci. USA* **112**, 6931-6936 (2015).
4. T. Iizumi, N. Ramankutty, How do weather and climate influence cropping area and intensity? *Glob. Food Secur.* **4**, 46-50 (2015).
5. C. Zhao, B. Liu, S. Piao, X. Wang, D. B. Lobell, Y. Huang, M. Huang, Y. Yao, S. Bassu, P. Ciais, Temperature increase reduces global yields of major crops in four independent estimates. *Proc. Natl. Acad. Sci. USA* **114**, 9326-9331 (2017).
6. S. Asseng, I. Foster, N. C. Turner, The impact of temperature variability on wheat yields. *Glob. Change Biol.* **17**, 997-1012 (2011).
7. H. Zhao, L. Zhang, M. Kirkham, S. M. Welch, J. W. Nielsen-Gammon, G. Bai, J. Luo, D. A. Andresen, C. W. Rice, N. Wan, US winter wheat yield loss attributed to compound hot-dry-windy events. *Nat. Commun.* **13**, 7233 (2022).
8. C. Lesk, P. Rowhani, N. Ramankutty, Influence of extreme weather disasters on global crop production. *Nature* **529**, 84-87 (2016).
9. M. Glotter, J. Elliott, Simulating US agriculture in a modern Dust Bowl drought. *Nat. Plants* **3**, 1-6 (2016).
10. S. M. Kim, R. Mendelsohn, Climate change to increase crop failure in US. *Environ. Res. Lett.* **18**, 014014 (2023).
11. D. Wei, J. A. Gephart, T. Iizumi, N. Ramankutty, K. F. Davis, Key role of planted and harvested area fluctuations in US crop production shocks. *Nat. Sustain.*, 1-9 (2023).
12. F. Schierhorn, D. Müller, A. V. Prishchepov, M. Faramarzi, A. Balman, The potential of Russia to increase its wheat production through cropland expansion and intensification. *Glob. Food Sec.* **3**, 133-141 (2014).
13. R. P. Lollato, G. P. Bavia, V. Perin, M. Knapp, E. A. Santos, A. Patrignani, E. D. DeWolf, Climate-risk assessment for winter wheat using long-term weather data. *J. Agron.* **112**, 2132-2151 (2020).
14. I. Hashmiu, O. Agbenyega, E. Dawoe, Determinants of crop choice decisions under risk: A case study on the revival of cocoa farming in the Forest-Savannah transition zone of Ghana. *Land Use Policy* **114**, 105958 (2022).
15. Q. Zheng, T. Ha, A. V. Prishchepov, Y. Zeng, H. Yin, L. P. Koh, The neglected role of abandoned cropland in supporting both food security and climate change mitigation. *Nat. Commun.* **14**, 6083 (2023).

16. T. Iizumi, I.-E. A. Ali-Babiker, M. Tsubo, I. S. Tahir, Y. Kurosaki, W. Kim, Y. S. Gorafi, A. A. Idris, H. Tsujimoto, Rising temperatures and increasing demand challenge wheat supply in Sudan. *Nat. Food* **2**, 19-27 (2021).
17. O. S. Obembe, N. P. Hendricks, J. Tack, Decreased wheat production in the USA from climate change driven by yield losses rather than crop abandonment. *PloS One* **16**, e0252067 (2021).
18. X. Cui, Beyond yield response: weather shocks and crop abandonment. *J. Assoc. Environ. Res. Econ.* **7**, 901-932 (2020).
19. A. S. Cohn, L. K. VanWey, S. A. Spera, J. F. Mustard, Cropping frequency and area response to climate variability can exceed yield response. *Nat. Clim. Change* **6**, 601-604 (2016).
20. J. R. Porter, L. Xie, A. J. Challinor, K. Cochrane, S. M. Howden, M. M. Iqbal, D. B. Lobell, M. I. Travasso, *Food security and food production systems*. (Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change., Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA, 2014), pp. 485-533.
21. L. Breiman, Random forests. *Mach. Learn.* **45**, 5-32 (2001).
22. J. Romm, The next dust bowl. *Nature* **478**, 450-451 (2011).
23. S. D. Schubert, M. J. Suarez, P. J. Pegion, R. D. Koster, J. T. Bacmeister, On the cause of the 1930s dust bowl. *Science* **303**, 1855-1859 (2004).
24. L. S. Shapley, A value for n-person games. *Contrib. Theor. Games*, (1953).
25. A. Dai, Drought under global warming: a review. *Wiley Interdiscip. Rev. Clim. Change* **2**, 45-65 (2011).
26. B. I. Cook, R. L. Miller, R. Seager, Amplification of the North American “Dust Bowl” drought through human-induced land degradation. *Proc. Natl. Acad. Sci. USA* **106**, 4997-5001 (2009).
27. A. Kumar, M. Chen, Understanding skill of seasonal mean precipitation prediction over California during boreal winter and role of predictability limits. *J. Clim.* **33**, 6141-6163 (2020).
28. M. L. L'Heureux, A. F. Levine, M. Newman, C. Ganter, J. J. Luo, M. K. Tippett, T. N. Stockdale, *ENSO prediction* (El Niño Southern Oscillation in a changing climate, Washington, DC: American Geophysical Union, 2020), pp. 227-246.
29. F. Rembold, M. Meroni, F. Urbano, G. Csak, H. Kerdiles, A. Perez-Hoyos, G. Lemoine, O. Leo, T. Negre, ASAP: A new global early warning system to detect anomaly hot spots of agricultural production for food security analysis. *Agric. Syst.* **168**, 247-257 (2019).
30. N. Rayner, D. E. Parker, E. Horton, C. K. Folland, L. V. Alexander, D. Rowell, E. C. Kent, A. Kaplan, Global analyses of sea surface temperature, sea ice, and night marine air temperature since the late nineteenth century. *J. Geophys. Res. Atmos.* **108**, (2003).
31. R. Bain, T. R. Fortenbery, Impact of crop condition reports on national and local wheat

- markets. *J. Agric. Appl. Econ.* **49**, 97-119 (2017).
32. W. S. Cleveland, S. J. Devlin, Locally weighted regression: an approach to regression analysis by local fitting. *J. Am. Stat. Assoc.* **83**, 596-610 (1988).
 33. S. M. Lundberg, G. Erion, H. Chen, A. DeGrave, J. M. Prutkin, B. Nair, R. Katz, J. Himmelfarb, N. Bansal, S.-I. Lee, From local explanations to global understanding with explainable AI for trees. *Nat. Mach. Intell.* **2**, 56-67 (2020).
 34. R. R. Heim Jr, A review of twentieth-century drought indices used in the United States. *B. Am. Meteorol. Soc.* **83**, 1149-1166 (2002).
 35. C. B. Barber, D. P. Dobkin, H. Huhdanpaa, The quickhull algorithm for convex hulls. *ACM Trans. Math. Softw.* **22**, 469-483 (1996).
 36. E. Dickin, D. Wright, The effects of winter waterlogging and summer drought on the growth and yield of winter wheat (*Triticum aestivum* L.). *Eur. J. Agron.* **28**, 234-244 (2008).
 37. W. Anderson, R. Seager, W. Baethgen, M. Cane, Life cycles of agriculturally relevant ENSO teleconnections in North and South America. *Int. J. Climatol.* **37**, 3297-3318 (2017).
 38. S. D. Schubert, M. J. Suarez, P. J. Pegion, R. D. Koster, J. T. Bacmeister, Causes of long-term drought in the US Great Plains. *J. Clim.* **17**, 485-503 (2004).
 39. K. C. Mo, Interdecadal modulation of the impact of ENSO on precipitation and temperature over the United States. *J. Clim.* **23**, 3639-3656 (2010).
 40. T. Iizumi, J.-J. Luo, A. J. Challinor, G. Sakurai, M. Yokozawa, H. Sakuma, M. E. Brown, T. Yamagata, Impacts of El Niño Southern Oscillation on the global yields of major crops. *Nat. Commun.* **5**, 3712 (2014).
 41. C. Bren d'Amour, L. Wenz, M. Kalkuhl, J. C. Steckel, F. Creutzig, Teleconnected food supply shocks. *Environ. Res. Lett.* **11**, 035007 (2016).
 42. D. K. Ray, N. D. Mueller, P. C. West, J. A. Foley, Yield trends are insufficient to double global crop production by 2050. *PloS One* **8**, e66428 (2013).
 43. R. Fischer, D. Byerlee, G. Edmeades, Crop yields and global food security. *ACIAR*, 8-11 (2014).
 44. S. P. Long, A. Marshall-Colon, X.-G. Zhu, Meeting the global food demand of the future by engineering crop photosynthesis and yield potential. *Cell* **161**, 56-66 (2015).
 45. S. Zhou, B. Yu, Y. Zhang, Global concurrent climate extremes exacerbated by anthropogenic climate change. *Sci. Adv.* **9**, eabo1638 (2023).
 46. K. P. Tripathy, S. Mukherjee, A. K. Mishra, M. E. Mann, A. P. Williams, Climate change will accelerate the high-end risk of compound drought and heatwave events. *Proc. Natl. Acad. Sci. USA* **120**, e2219825120 (2023).

Chapter 3 - Breeding in U.S. winter wheat: a four-decade decline in climate resilience

3.1. Introduction

Global wheat production faces mounting challenges from increasing demand by population growth and the threat of climate extremes¹⁻⁴. Drought and heat extremes are estimated to cause wheat production losses of approximately 10%^{5,6}, with even greater declines observed during compound hot-dry (HD) events, where both conditions occur simultaneously⁷⁻⁹. Such compound events could cause global crop yield losses of up to 30%⁷, highlighting the urgent need for breeding strategies that enhance climate resilience.

Climate resilience, as defined by the Intergovernmental Panel on Climate Change (IPCC) Special Report on Climate Extremes (SREX, 2012), refers to a system's capacity to anticipate, absorb, accommodate, or recover from climatic shocks while preserving core function¹⁰. In a breeding context, resilience denotes the ability of cultivars to maintain stable and consistent yield improvements under different stress levels¹¹⁻¹³ (Figure B.1a). Achieving this requires that cultivar advancements improve tolerance to climatic extremes¹⁴ such as HD events, thus buffering against climate-related shocks and minimizing yield loss^{15,16} (Figure B.1b). Retrospective analysis of cultivar performance across historical trials is therefore essential for understanding how past breeding efforts have shaped climate resilience and guiding future strategies¹².

Recent studies have explored breeding-driven changes in climate resilience using different approaches. These include analyzing crossover patterns of genotype-environment interactions across global wheat trials¹⁷, tracking temporal evolution of response diversity in European wheat cultivars¹⁸, and assessing heat sensitivity in U.S.^{6,19} and South African²⁰ wheat (Figure B.2). While these efforts have yielded valuable insights, their conclusions remain inconsistent. For example,

Kahiluoto et al. (2019)¹⁸ argued that declining response diversity in European wheat cultivars has weakened climate resilience, whereas others²¹ have argued that reduced diversity does not necessarily imply diminished resilience. Similarly, in the U.S. hard winter wheat (HWW) region, some studies reported that newer cultivars are more sensitive to extreme heat than older cultivars⁶, while others reported the opposite¹⁹.

These discrepancies partly stem from the limitations of data availability and quality. Most prior studies lacked long-term, cultivar-specific yield datasets across diverse environmental conditions, a critical requirement for detecting genotype-environment interactions and quantifying cultivar-specific tolerance to climatic extremes²². Due to these constraints, some studies have primarily relied on clustering cultivars by release years to infer changes in resilience^{6,19}. However, this may confound resilience estimates when multiple cultivars were released in the same year. Furthermore, prior studies have focused mainly on single climatic extreme events such as heat, with few explicitly examining cultivar-specific responses to compound HD events. This underscores a critical gap, as HD events trigger unique and synergistic physiological responses that cannot be inferred from individual stressors alone^{23,24}. Such compound events have also been shown to cause more severe wheat yield losses than heat or drought alone^{7,9}. Consequently, whether historical breeding has improved resilience to HD events remains a largely underexplored question.

Rainfed cultivar performance trials conducted by land-grant universities across the U.S. HWW belt (Figure 3.1a) provides an opportunity to fill these knowledge gaps. As the world's largest contiguous low-rainfall wheat-producing region, the HWW belt has experienced substantial climatic variability in recent decades. Despite overall yield gains, the region faces rising climate risks. Notably, yield instability, measured as the coefficient of variation, has increased by

2% per decade (Figure 3.1b), signaling heightened vulnerability. Without targeted improvements in tolerance to compound extremes, such as those exemplified by the 1930s Dust Bowl, continued climate variability could undermine regional production and ripple through global food supply.

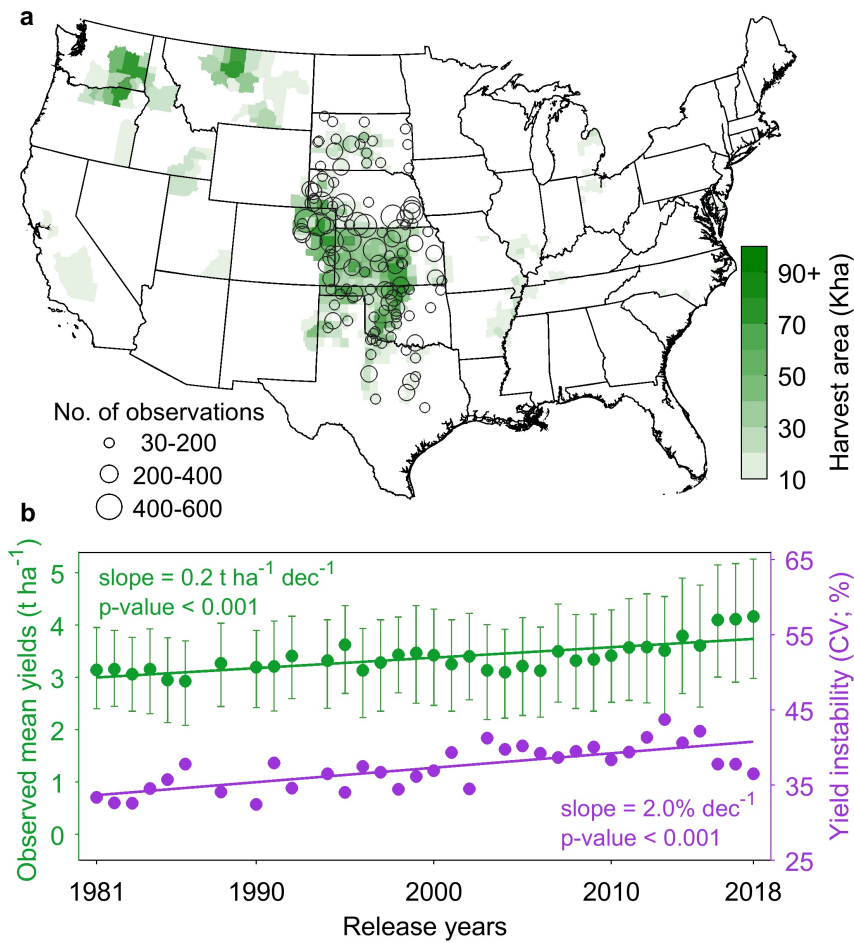


Figure 3.1. Yield and yield instability of winter wheat cultivars released from 1981 to 2018 in the U.S. winter wheat belt. a, Winter wheat cultivar trial sites, numbers of observations, and harvested area (Kha). The circles represent 119 trial locations, with the size of the circles indicating the number of year-cultivar observations. The background colors show county-level averaged harvested area over 1982-2020 across the U.S. obtained from the U.S. Department of Agriculture, National Agricultural Statistics Service (USDA-NASS). b, Mean wheat yield (green) and its coefficient of variation (CV, purple) across the cultivar release years. Higher CV suggests more instable yield. The error bars in observed yields show mean $\pm$ one standard deviation among all cultivars released in the same year (the average number of observations for each release year is 725). Both solid lines are linear regression trends based on the Mann-Kendall test.

Here, we compiled a comprehensive dataset of rainfed field trials across six U.S. HWW states (Table B.1), encompassing 150 cultivars released between 1981 and 2018. The dataset

includes 25,359 yield observations, with each cultivar tested in 169 site-years on average. These cultivars were widely adopted by local farmers, reflecting real-world breeding progress. This study aims to: (1) Determine whether historical breeding programs have improved climate resilience across varying environmental stress levels. The stress levels are quantified by the environmental index (EI), calculated as the average yield of all cultivars for a given site-year²⁵; (2) Assess temporal patterns in cultivar-specific responses to HD events; and (3) Quantify cultivar-specific HD tolerance and yield performance, which provide actionable insights to guide future breeding strategies.

To focus our analysis on critical periods of wheat development, we divided the HWW life cycle into three phenological periods for each site-year: planting to jointing (p1), jointing to heading (p2), and heading to maturity (p3) (Supplementary Text B.1 and Figure B.3). Given that HD events routinely occur during the grain filling period (p3) of wheat and detrimentally impact yield^{9,23} by causing nitrogen loss, shortening the grain-filling duration, and reducing grain weight^{9,26}, we focus on the impacts of HD during this period (see Methods). Emerging evidence highlights atmospheric dryness, characterized by rapid increases in atmospheric water demand, can severely affect plants^{8,27} even when the soil water supply is adequate²⁸. In particular, low relative humidity has been identified as a key factor in evaluating the impacts of atmospheric dryness^{8,29}. Accordingly, we defined HD events based on daily maximum temperature (Tx) and minimum relative humidity (RHn).

3.2. Material and Methods

3.2.1 Crop data

Raw winter wheat data including observed dryland cultivar yields (average of three to four

replications), and phenology (planting and harvest dates) were collected and digitized from printed or online publicized State Winter Wheat Performance Test Reports from 1982 to 2020 across South Dakota, Nebraska, Colorado, Kansas, Oklahoma, and Texas, which collectively account for approximately 50% of the U.S. wheat harvested area³⁰ (Figure 3.1a). The observed phenology was used to segment the life cycle of winter wheat into three key phenological periods: planting to jointing (p1), including crop establishment, tillering, and winter survival, predominately occurs in late fall, winter, and early spring; jointing to heading (p2), including spike formation and development, stem elongation, and leaf development, occurs during mid-spring; heading to maturity (p3), determining actual grain number and weight³¹ in later spring and early summer (Supplementary Text B.1 and Figure B.3). In addition, the commercial release years for each cultivar was taken from “The Wheat Farmer” (Table B.1), a professional publication for farmers and agriculture businesses in the U.S. hard winter wheat belt. Our analysis focused on 150 hard winter wheat cultivars released from 1981 to 2018, each with at least 50 site-year observations across 119 trial locations that conducted field trials for at least five years (a total of 25,359 observations), ensuring the reliability of our analysis. Crop data sources are shown in Table B.1.

3.2.2 Climate data

Daily maximum temperature (Tx, °C), minimum temperature (Tn, °C), minimum relative humidity (RHn, %), and precipitation (Prcp, mm) from 1982-2020 were retrieved at a 4-km spatial resolution from the gridded meteorological (gridMET) dataset³² (Table B.1). The gridMET dataset integrates two distinct datasets [temporally rich data from the North American Land Data Assimilation System Phase 2 (NLDAS-2) and spatially rich data from the Parameter-elevation Regressions on Independent Slopes Model (PRISM)]. It has been validated using an extensive

network of weather stations across the U.S.³².

3.2.3 Yield gains through cultivar advancements across varying levels of environmental stress

To ensure a robust and valid assessment of how breeding-driven yield gains vary across different environmental stress levels, we identified 58 cultivar subsets (or groups) that met stringent temporal and spatial coverage criteria, based on a structured six-step selection procedure (Supplementary Text B.3; Figures B.4 and B.10a). Each group includes cultivars released over at least 10 distinct years and tested across at least 10 environments (site-years), ensuring consistent cultivar evaluations across a broad range of environmental conditions. For example, one representative group (Figure B.5a) included 16 cultivars released between 1988 and 2010 across 30 environments. Together, these 58 groups comprise 118 distinct cultivars released between 1984 and 2018, representing 79% of all cultivars in our dataset.

Next, we estimated the breeding-driven yield trends across different stress levels, based on all 58 group datasets. Taking one group (Figure B.5a) as an example, we calculated an environmental index (EI) for each site-year, defined as the average yield of all cultivars in that site-year²⁵ (blue dots in Figure B.5b). The EI provided a localized indicator of growing conditions that reflects the integrated effects of weather, soil conditions, and management practices. We then estimated the breeding-driven yield trends (or gains) ($\frac{\partial Yield}{\partial RY}$; red dots in Figure B.5b) for each site-year by a simple linear regression of cultivar yields against their release years (RY). Lastly, we examined the relationship between the breeding-driven yield trends and EI across all environments, i.e., yield trends at the Y-axis and EI at the X-axis shown in Figure B.5c. We repeated this analysis for all 58 groups. To determine the overall response of cultivar advancement

to varying environmental conditions across all groups, we used a linear mixed-effects model with breeding-driven yield trends as the response variable, EI as a predictor, and cultivar group as a random effect to account for group-level variation.

To further assess cultivar progress-driven yield changes, we selected a long-term wheat cultivar ‘Arapahoe,’ released in 1988 with the longest trial period among all cultivars studied, as a reference cultivar. This reference cultivar was widely planted in 438 site-years (Figure B.10b). To ensure reliable comparisons of cultivar performance across diverse environments, we conducted the following three-step analysis (Supplementary Text B.4). (1) Environmental classification: Each site-year was classified as a low-, moderate-, or high-yielding environment by comparing Arapahoe’s yield in that site-year against its 25th and 75th percentile yields across all 438 site-years (Figure B.6a). (2) Yield adjustment: To reduce confounding effects from environmental variability, we normalized cultivar yields relative to Arapahoe’s yield. Specifically, for each site-year, the yield of a given cultivar was adjusted by adding the deviation between Arapahoe’s average yield under the corresponding environmental types (i.e., low- or high-yielding) and Arapahoe’s observed yield in that site-year (Figure B.6b-f). This adjustment standardized yield comparisons across site-years, enabling clearer isolation of breeding-driven yield effects. (3) Yield trend estimation for low- and high-yielding environments: To ensure fair comparisons, we retained only cultivars that were observed in both environmental types within the same release year (Figure B.6g,h). Breeding-driven yield trends across release years were then estimated separately for low- and high-yielding environments (Figure B.6i). Although older and advanced cultivars were compared within the same environmental type, a more rigorous approach would involve testing all cultivars together in the same site-years across a broad range of environments to most accurately estimate breeding-driven yield trends under low- and high-

yielding environments.

3.2.4 Compound hot-dry extreme events

During p1 and p2 periods in winter wheat, the 85th percentile of daily maximum temperatures from 1982 to 2020 at each site remained below 32°C (Figure B.11), a threshold typically associated with heat stress³³, making hot-dry events rare⁹. Hot-dry events during the p3 period, however, have increased^{9,34,35} due to climate change and tend to cause significant yield reductions^{9,26,34}. Therefore, our analysis focuses on the compound hot-dry extremes (HD) during p3 period associated with wheat yields. A HD event was defined as a day (d) when Tx exceeded 32°C^{9,33} and RHn fell below 30% simultaneously^{9,36} (Figure B.7). We then calculated the frequency of HD events during this period for each site-year as,

$$HD (\%) = \frac{\sum_{d=1}^N HD_d}{N} \times 100 \quad HD_d = \begin{cases} 1, & \text{if } Tx_d \geq 32^\circ\text{C and } RHn_d \leq 30\% \\ 0, & \text{otherwise} \end{cases} \quad (1)$$

where N is the total number of days during the p3 period.

3.2.5 Regression Model

A linear mixed-effects model³⁷ was used to isolate the effects of time-invariant factors and the main climate effects. While we do not directly account for these time-invariant factors such as soil quality, we control them using site random effects. We also included cultivar and trial year random effects. The cultivar effect directly controls genetic gains over time from breeding efforts, and the trial year effects account for the changes in technology and management practices. The model is specified as:

$$Y_{c,l,t} = \alpha_c + \alpha_l + \alpha_t + f(W_{c,l,t}; \beta) + \delta HD_{c,l,t} + \varepsilon_{c,l,t} \quad (2)$$

$$\begin{aligned}
f(W_{c,l,t}; \beta) = & \sum_{p=1}^3 \beta_{1,p} GDD_{c,l,t,p} + \sum_{p=1}^2 \beta_{2,p} FDD_{c,l,t,p} + \sum_{p=2}^3 \beta_{3,p} EDD_{c,l,t,p} + \sum_{p=1}^3 \beta_{4,p} Prcp_{c,l,t,p} \\
& + \sum_{p=1}^3 \beta_{5,p} Prcp_{c,l,t,p}^2
\end{aligned} \tag{3}$$

where $Y_{c,l,t}$ is yield for cultivar “ c ” at location “ l ” in trial year “ t ”. The first three terms ($\alpha_c, \alpha_l, \alpha_t$) are controls, including cultivars, locations, and trial years. The $f(W_{c,l,t}; \beta)$ represents the effects of specific climate covariates (W with the corresponding coefficient β), including growing degree days (GDD , °C days), freezing degree days (FDD , °C days), extreme degree days (EDD , °C days), and a linear and quadratic term for total precipitation ($Prcp$, mm) during specific phenological periods (Supplementary Text B.2), which together capture the nonlinear yield responses to temperature and precipitation. Note, for reducing overall degrees of freedom, the FDD_{p3} and EDD_{p1} were not included in our model due to their uncommon occurrence in actual climate conditions⁹. To ensure independent estimation of HD and EDD effects during the p3 period, we used an adjusted EDD_{p3} by excluding days that overlapped with HD events. The δ represents the average sensitivity of wheat yields to 1% of HD exposure. It is likely that the error term $\varepsilon_{c,l,t}$ is heteroskedastic and autocorrelated. Therefore, we cluster standard errors (SEs)³⁸ by cultivar-year, allowing us to consider the effects of heteroskedastic and autocorrelation in estimating coefficients. The adjusted SEs enabled the production of more conservative adjusted p-values (Table B.3).

A model that logarithmically transformed yields was also tested, and all the results were similar to those using raw yields. Our preferred specification used original yields because the model presented more explanatory power and more normally distributed residuals. Next, a variance inflation factor (VIF)³⁹ was conducted to evaluate the risk of multicollinearity. The VIF

values for all temperature indices are less than 2, indicating our model does not have a serious multicollinearity problem.

3.2.6 Changes in sensitivity to HD throughout cultivar progression

We employed three methods to assess the change in HD sensitivity during cultivar progress. 1) Partitioning by HD frequency bins: To account for spatial and temporal differences (i.e., soil and management), we divided yield observations within each state and decade into four frequency bins based on HD occurrence: 0th-25th, 25th-50th, 50th-75th, and 75th-100th percentiles. Yield observations within the same bin were pooled, and yield trends over cultivar release years were then estimated separately for each bin (Figure 3.3a). 2) Iterative cultivar group analysis: We created 435 cultivar observation groups through iterating one-year increments on a basis of ten release years from the oldest cultivar group (1981-1990) to the newest one (2009-2018) (i.e., 1981-1990, 1981-1991, 1981-1992, ..., 2009-2018 which are shown in Figure 3.3b). Then, we applied the model (Eq. 2) separately to each cultivar group to assess HD sensitivity. Note that the specific subsets of the dataset used for different analyses are shown in Table B.6. 3) Multilevel modeling of HD sensitivity: To estimate the sensitivity of each cultivar to HD (δ_c), we extended the model (Eq. 2) using a multilevel model⁴⁰ that included the interactions between HD and dummy variables for the cultivars. This allowed us to demonstrate the trajectory of HD sensitivity over the cultivar advancements (Figure 3.3c).

3.2.7 Variability of cultivar performances

To assess the performance of individual cultivars by simultaneously accounting for their response to HD stress and yield potential under historical climatic conditions, we conducted three

steps. 1) We first applied a bootstrap approach with 500 simulations to the cultivar $\times$ HD interaction model. We randomly sampled data 500 times, ensuring that the same data length was extracted for each cultivar in every sampling. This process generated 500 distinct datasets (each containing 25,359 data points), which were used to repeatedly run the model producing 500 independent model structures. 2) We then estimated the mean yield of each cultivar, representing its yield potential, based on each bootstrapped model structure. To enable meaningful comparisons of yield across cultivars experiencing different environmental conditions, we simulated the mean yield ($\hat{\mu}_c$) for each cultivar based on the average sampled climate conditions ($\bar{W}$ and $\overline{HD}$) as,

$$\hat{\mu}_c = \alpha_c + \bar{\alpha}_l + \bar{\alpha}_t + f(\bar{W}; \beta) + \delta_c \overline{HD} \quad (4)$$

The α_c is cultivar-specific fixed effects; $\bar{\alpha}_l$ and $\bar{\alpha}_t$ are average site and year effects, respectively. In total, the analysis resulted in 75,000 data points (150 cultivars $\times$ 500 simulation). 3) We categorized all cultivar performances into four groups based on the average values of HD sensitivity and simulated yield. These four groups are ‘high yield potential and HD-tolerant,’ ‘low yield potential and HD-tolerant,’ ‘high yield potential and HD-sensitive,’ and ‘low yield potential and HD-sensitive.’

3.2.8 Robustness checks

To verify our findings, we conducted a series of additional analyses. Specifically, we recalculated HD events using an alternative definition based on site-level relative percentile thresholds. A HD event was defined as a day during the p3 period when Tx exceeded the 85th percentile of the local Tx distribution and RHn simultaneously fell below the 15th percentile of the local RHn distribution. Using this definition, we re-estimated the model (Eq. 2), and the results consistently showed that HD events led to significant wheat yield reductions (Figure B.12a).

To validate the decline in HD resilience with cultivar advancements, we tested seven alternative modeling structures: (1) We re-estimated the cultivar $\times$ HD interaction model using the alternative HD definitions mentioned above (Figure B.12b). (2-5) Based on the preferred model, we tested two extended models with additional interaction terms: the first model allowed the effects of both EDD_{p3} and HD to vary across cultivars, and the second one allowed the effects of all climate indices (GDD, FDD, EDD, Prcp, and HD) to vary across cultivars. We also tested two temperature-quadratic models that replaced all temperature indices (GDD, FDD, and EDD) with linear and quadratic terms of average temperature during three phenological periods to estimate the changes in HD sensitivity when allowing either HD effects alone or all climate effects to vary across cultivars (Figure B.13 and Table B.5). (6) We re-ran the preferred model but used relative yield as the response variable. Relative yield ($RY_{c,e}$; %) for cultivar c in environment e was calculated as $\frac{(Y_{c,e} - \hat{Y}_c)}{\hat{Y}_c} \times 100$, where $Y_{c,e}$ is the observed yield, and $\hat{Y}_c$ is the average yield of cultivar c across all environments (or site-years) (Figure B.14). (7) While our model included a site random effect to account for soil-related influences on yield, we also tested whether explicitly incorporating site-level soil properties would affect our results by adding either soil texture or available water capacity (AWC) as a covariate to the preferred model (Figure B.15). Across all alternative models, we consistently found a robust pattern of declining HD resilience over breeding progress.

3.3. Results

3.3.1 Change in climate resilience over wheat breeding

To evaluate whether breeding has improved climate resilience, we analyzed yield trends with cultivar advancements under varying environmental stress levels. The stress level was

quantified using the EI, where higher values represent more favorable environments for wheat

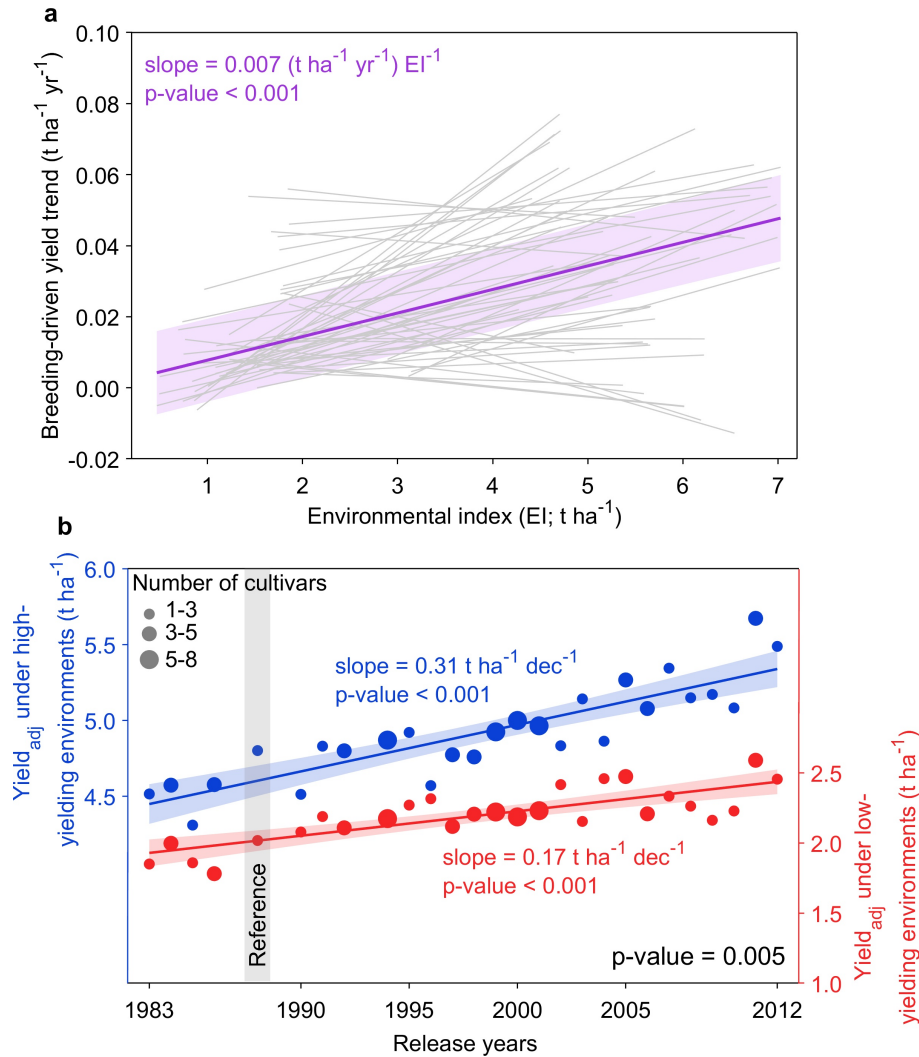


Figure 3.2. Wheat cultivar response to environmental stress. a, Breeding-driven yield trends against the environmental index (EI; t ha^{-1}) for 58 groups (gray lines). The purple line represents the overall relationship between yield trends and EI across all groups, with shaded bands indicating the 95% confidence interval. b, Changes in adjusted yield based on the reference cultivar ‘Arapahoe’ over the cultivar release years under both high- (blue) and low-yielding (red) environments. The size of the circle shows the number of cultivars. Solid lines and shaded areas are yield trends and the 95% confidence intervals, respectively. The gray shaded region marks the reference cultivar ‘Arapahoe.’ The p-value in black font denotes the statistical significance of the difference in yield trends between low- and high-yielding environments, based on analysis of covariance.

development and yield. A key requirement for this analysis is the simultaneous testing of cultivars from different release years across a range of environmental conditions. To meet this criterion, we constructed 58 cultivar groups (Figure B.4; Methods), each comprising cultivars released across

at least 10 distinct years and consistently tested in at least 10 site-years (i.e., Figure B.5). Across all groups, our analysis revealed a significant positive relationship between breeding-driven yield trends and EI (p-value < 0.001; purple line in Figure 3.2a; Methods), indicating that yield gains from breeding have been substantially greater in favorable environments than in stressed environments. For example, average yield gains were minimal ($0.10 \text{ t ha}^{-1} \text{ dec}^{-1}$) in stressed environments (i.e., $\text{EI} < 2 \text{ t ha}^{-1}$) but reached up to $0.50 \text{ t ha}^{-1} \text{ dec}^{-1}$ in favorable conditions (i.e., $\text{EI} > 6 \text{ t ha}^{-1}$) (Figure 3.2a). This pattern suggests that current breeding programs are less effective at enhancing yield gains under adverse environments, indicating a decline in climate resilience (Figure B.1a).

To verify this finding, we used ‘Arapahoe,’ a HWW cultivar released in 1988 and consistently planted until 2012, the longest-running cultivar in our dataset, as a reference cultivar. Using its yield performance as a benchmark, we classified 438 site-years where ‘Arapahoe’ was grown into two environmental types (low- and high-yielding) (Supplementary Text B.4; Methods). To enable more reliable comparisons of cultivar yields across different site-years within each environmental type, we adjusted yields to a normalized condition based on the reference cultivar yield (Supplementary Text B.4; Methods). Analysis on the yield trends with cultivar advancement (Figure B.6; Methods) revealed that, while the new cultivars have improved yields, the rate of yield improvement in a high-yielding environment ($0.31 \text{ t ha}^{-1} \text{ dec}^{-1}$) was nearly twice that found in a low-yielding environment ($0.17 \text{ t ha}^{-1} \text{ dec}^{-1}$) (Figure 3.2b), and this difference in their rates was statistically significant (p-value = 0.005; Figure 3.2b). These consistent patterns (Figure 3.2) imply that newer cultivars may be more sensitive to climatic extremes such as compound HD events, incurring greater yield losses under poor growing conditions (Figure B.1b).

3.3.2 Breeding-driven change in HD resilience

Compound HD events, days with simultaneously high temperature and atmospheric dry conditions, have been identified as a major threat to wheat yield in the U.S. HWW belt⁹, potentially contributing to low-yielding environments. Therefore, we evaluated whether the diminished climate resilience (Figure 3.2) was specifically driven by reduced resilience to HD events.

We first confirmed the impact of HD events on wheat yield. Using site-specific historical climate data, we defined an HD event during the critical p3 period as a day when daily Tx exceeded 32°C^{9,33} and RHn fell below 30% simultaneously^{9,36} (Figure B.7; Methods). To account for variation in the duration of the p3 period across sites and years, we calculated the frequency (%) of HD events during this period (Eq. 1). We then used a linear mixed-effects model to quantify the effect of HD events on wheat yield while accounting for multiple climate variables, including growing degree days, freezing degree days, extreme degree days, and precipitation (Eqs. 2 and 3; Supplementary Text B.2). A likelihood ratio test confirmed the significance of HD events as a predictor (p-value < 0.001; Table B.2). Specifically, a 1% increase in HD event was associated with a yield loss of 0.01 t ha⁻¹ (p-value < 0.001; Table B.3). Given an average HD occurrence of 14% across the U.S. HWW belt, this translates to a yield loss of 0.14 t ha⁻¹, equivalent to 6% of the regional mean yield (2.4 t ha⁻¹).

We next evaluated breeding-driven change in HD resilience using three approaches. First, we analyzed yield trends across the cultivar release years under varying HD stress levels. Although yield improved significantly from 1981 to 2018 across all HD stress levels (p-value < 0.05), the rate of improvement declined under higher HD stress levels (Figure 3.3a), echoing findings under varying environmental stresses (Figure 3.2). Under the highest HD stress level (>75th percentile bin), the yield trend was 79% lower than that under the lowest HD stress level (0-25th percentile

bin) (Figure 3.3a).

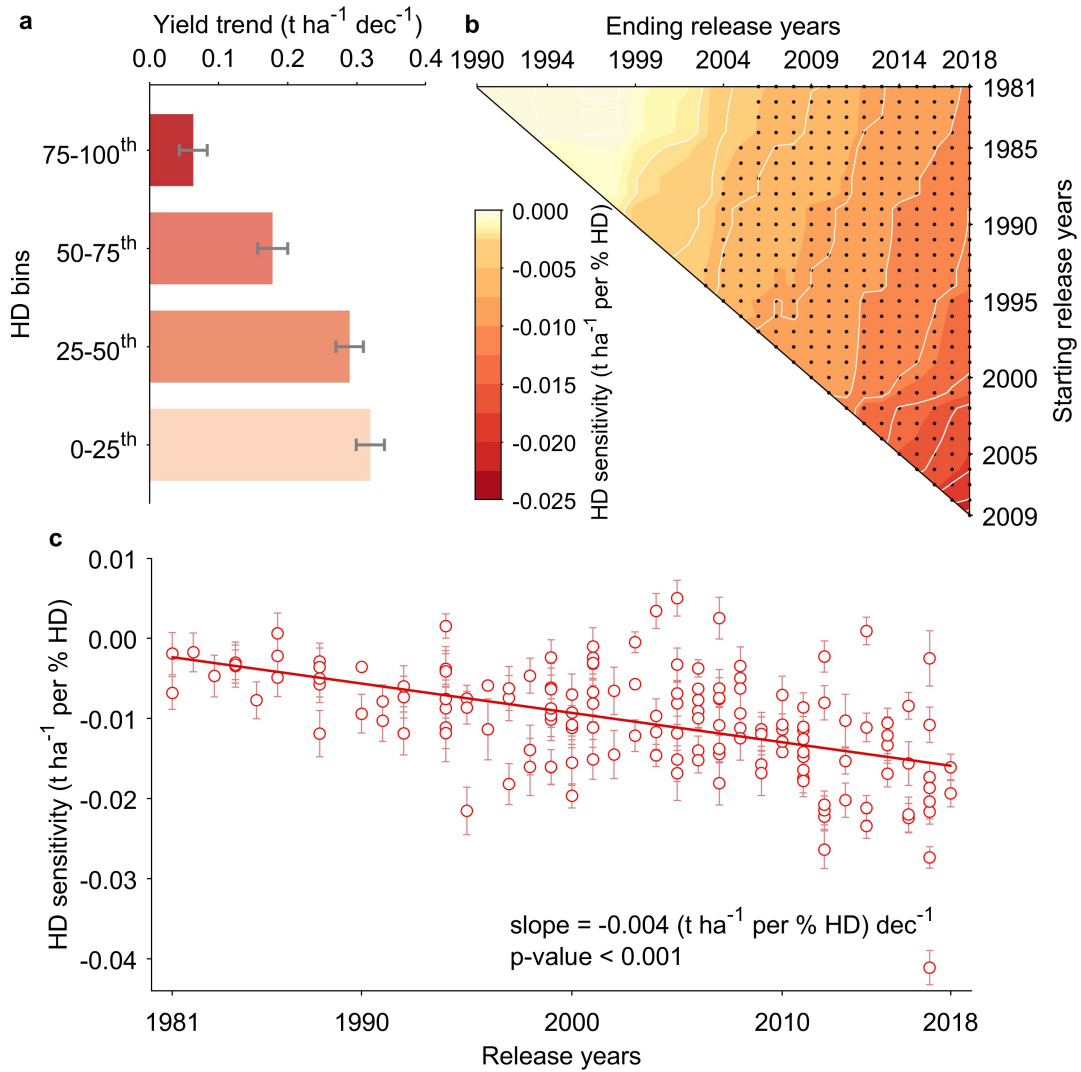


Figure 3.3. Sensitivity of winter wheat cultivar advancement to hot-dry events (HD). a, Yield trends across cultivar release years (horizontal bars) are presented across four HD percentile bins, with error bars representing the mean $\pm$ one standard error (SE). b, Average estimated HD sensitivity ($\text{t ha}^{-1} \text{per \% HD}$) of cultivars released over different time periods, with black dots indicating statistical significance at the 95% confidence level. c, Estimated HD sensitivity across all cultivars, where each open circle represents a newly released cultivar in the U.S. hard winter wheat belt. Error bars show mean $\pm$ one clustered SE. The solid red line represents the linear regression trend over cultivar release years.

Second, we applied our model (Eq. 2) to each of the 435 observation groups, which consisted of cultivars released within specific time windows, with a focus on evaluating the yield impact per 1% of HD events (Methods). Across all groups, the sensitivities to HD events were consistently negative, with a pronounced decline in more recently released cultivars (Figure 3.3b).

In particular, cultivars released during 2009-2018 exhibited the strongest sensitivity (-0.023 t ha^{-1} per 1% of HD events; Figure 3.3b). This pattern highlights an increasing vulnerability of newer cultivars to HD stress.

Third, to evaluate the cultivar-specific response to HD events, we incorporated genotype $\times$ environment interactions into our model using a varying-slope multilevel framework⁴⁰, allowing the effects of HD to vary across cultivars (Methods). 88% of the cultivars exhibited significant negative sensitivity to HD (Figure 3.3c). Furthermore, an increasingly negative sensitivity trend to HD was observed over breeding advancements, with an average decline of -0.004 t ha^{-1} per % HD per decade over 1981-2018 (Figure 3.3c). To explore possible sub-region disparities in breeding progress, we analyzed trends of HD sensitivity for each cultivar-source state where the wheat cultivars were developed (Table B.4). Our analysis showed the declining trends in HD tolerance across all states, especially in the Southern Great Plains States including Kansas (-0.005 t ha^{-1} per % HD per decade), Oklahoma (-0.007 t ha^{-1} per % HD per decade), and Texas (-0.004 t ha^{-1} per % HD per decade) (Figure B.8). These consistent patterns indicate that modern cultivars have become more sensitive to HD events. That is, newer cultivars experience larger yield losses per unit increase in HD events, reflecting breeding-driven decline in HD resilience (Figure B.1b).

3.3.3 Decadal and cultivar-specific variability in yield potential and HD tolerance

From the performance of 150 wheat cultivars (Methods), we found a trade-off between yield potential and HD tolerance over four decades, as illustrated by the negative trend in HD sensitivity with positive gains in yield potential (red line in Figure 3.4). This trade-off underscores the challenge of balancing crop yield with resilience to climatic extremes¹¹.

Distinct decadal patterns in the distribution of yield potential and HD sensitivity were

evident (Figure 3.4). Old cultivars (1981-1990) tended toward the lower end of yield potential and

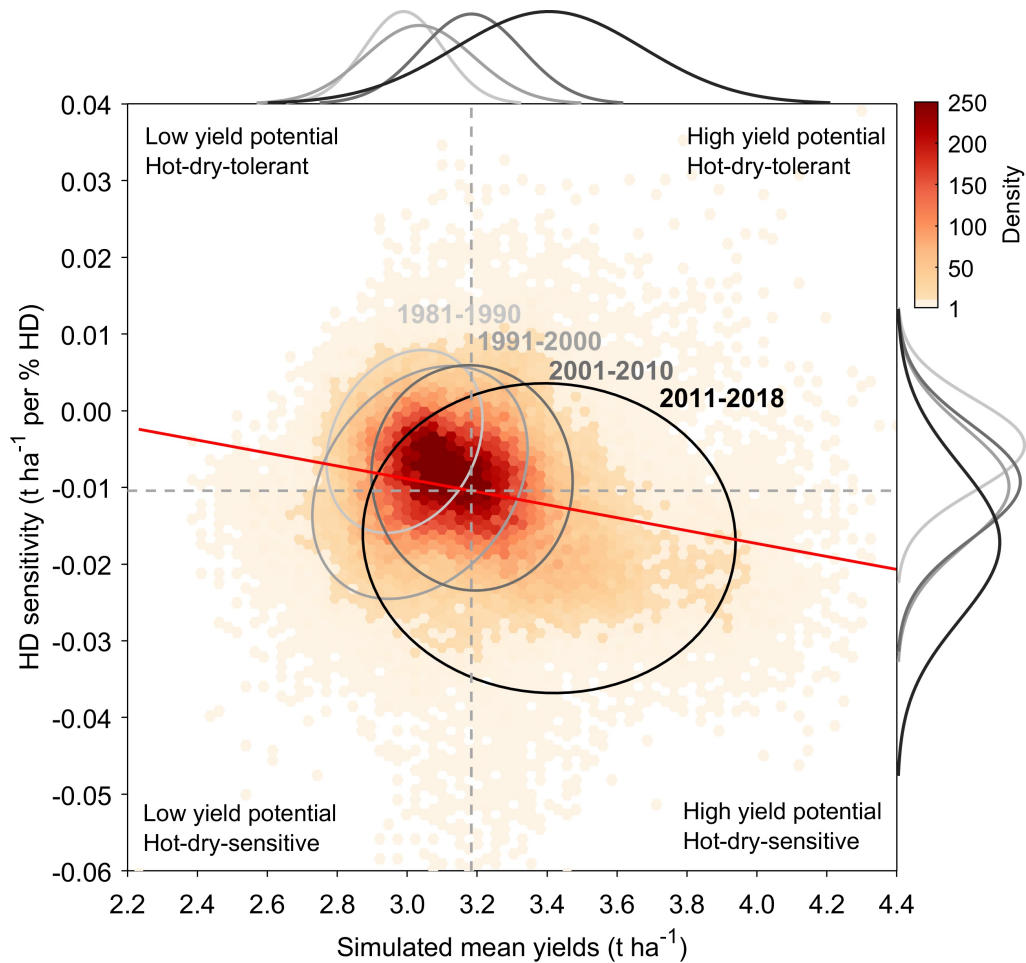


Figure 3.4. Decadal performance of winter wheat cultivars during release years from 1981 to 2018 based on sensitivity to hot-dry events (HD) versus the simulated mean yields. These estimations were conducted by bootstrapping the model 500 times. The simulated mean yields were derived from regressions under average climate conditions. The colorbar indicates the number of data points (totaling 150 cultivars $\times$ 500 bootstrap samples). The decadal 95% confidence ellipses (from light gray to black) (e.g., 1981-1990) of estimations illustrate their temporal tendency of high (low) yield potential and hot-dry-tolerant (-sensitive) cultivars by their release years. The solid red line represents an overall linear trend. The vertical dashed gray line indicates the average of all simulated yields while the horizontal dashed gray line shows the average of HD sensitivity. A set of histograms on the top and right are decadal distributions of mean yields and HD sensitivity, respectively, for each decadal cultivar.

higher HD tolerance. Specifically, 84% of cultivars exhibited low yield potential but high HD tolerance, while only 3% combined high yield potential with high HD tolerance (Figure 3.4). A shift occurred during 1991-2000, where 48% of cultivars still maintained low yield potential with

high HD tolerance, but 37% were categorized as low yield potential with high HD sensitivity (Figure 3.4). This result reflects a possible prioritization of other breeding objectives, such as disease and pest resistance⁴¹. Interestingly, cultivars released during 2001-2010 were more evenly distributed across four performance categories of yield potential and HD tolerance, indicating a

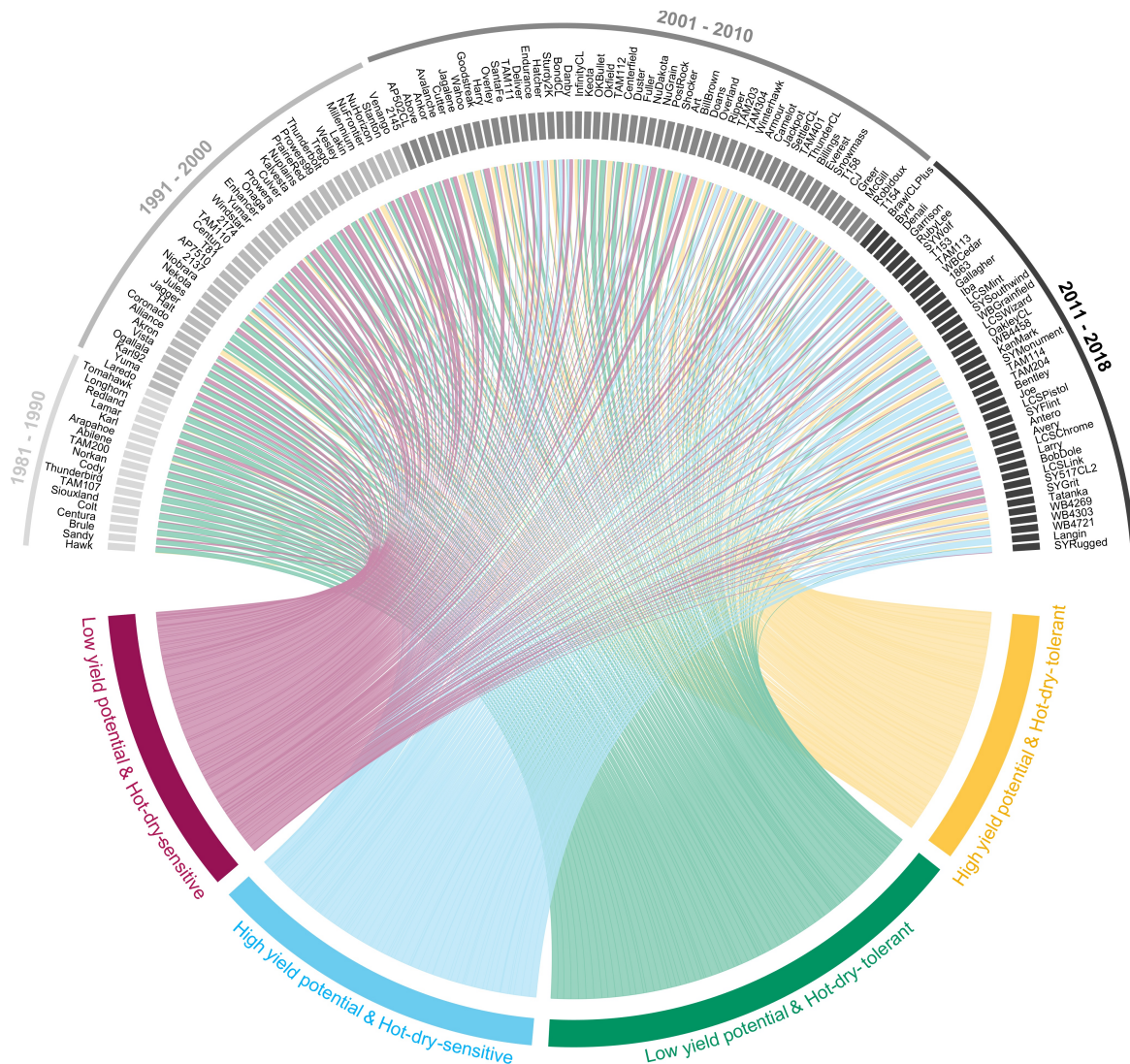


Figure 3.5. Probability of classifications among four combinations of yield potential (high and low) and hot-dry adaptation (-tolerant and -sensitive) for 150 cultivars released from 1981 to 2018. The width of each chord linking a cultivar and a classification represents the proportion of 500 bootstrap simulations indicating that the cultivar belongs to a specific classification. The decadal release years of cultivars are displayed clockwise on the top.

diversification of genetic traits (Figure 3.4). However, recent cultivars (2011-2018) exhibited a starkly different pattern: their yield potential centered higher, while the HD sensitivity distributions

became more negatively centered (Figure 3.4), reflecting increased susceptibility to HD events. Specifically, two-thirds of the cultivars were categorized as high yield potential and high HD sensitivity, and only 18% maintained both high yield potential and high HD tolerance. These findings underscore a critical cost associated with breeding progress: while breeders have optimized the yield potential, the associated loss of HD tolerance poses risks in stress-prone environments.

Analyzing cultivar-specific performance probabilities, we identified certain cultivars more likely to exhibit tolerance to HD events, such as ‘Jagger,’ an elite HWW cultivar in the U.S. (Figure 3.5 and Table B.4). The cultivar-specific differences are crucial for helping breeders in developing wheat cultivars with enhanced tolerance to HD events. For example, examining traits in cultivars like ‘Jagger’ can not only explore disease-resistance genes, but also identify novel candidate genes associated with HD tolerance. Additionally, a few HWW cultivars, such as ‘Overland,’ showed a higher probability of a combined high yield potential with high HD tolerance (Figure 3.5 and Table B.4). These findings highlight the opportunity to reorient breeding strategies toward balancing yield improvements with resilience to intensifying climatic extremes.

3.4. Discussion and Conclusion

The evaluation of breeding-driven HD resilience may be subject to several limitations. First, our analysis did not directly account for the influence of management practices such as fertilizer application and disease and pest control on wheat yield due to data limitations. The data reports we used, however, are designed as “best management practices,” aiming to minimize yield-reducing factors like nutrient deficiencies, and biotic stress. Additionally, our model incorporates year and site effects to account for unobserved factors, a common approach to control for spatial

and temporal variation^{9,42}. Second, while we used phenological data at the site-year level, incorporating cultivar-specific phenology could improve the analysis. Nonetheless, it seems that actual differences in heading dates among cultivars at each site-year are relatively small, around one day on average (Figure B.9). Third, studies have suggested that rising atmospheric CO₂ could potentially increase wheat yield by elevated CO₂ (eCO₂) fertilization effects and improved water use efficiency⁴³. However, this factor was not included in our analysis due to the considerable uncertainty in both modeling and observational eCO₂ effects on wheat yields⁴⁴.

Despite these limitations, our results robustly support two key conclusions. First, using the EI approach, we found that wheat breeding programs have reduced climate resilience over the past four decades. Cultivar-level analysis further revealed that while breeding has improved yield potential, it has not simultaneously enhanced HD resilience, suggesting an increasing interplay between genetics and environmental factors^{17,45,46}. Given the dominant role of temperatures in driving HD, the decreased HD resilience aligns with the finding that heat sensitivity of wheat yields in Kansas has increased in recent decades^{6,47}. Several factors may explain decreased tolerance to HD over breeding progress. (1) Breeders often assume that breeding progress inherently adapts to climatic change, as cultivar selections are typically conducted across environments with a constantly changing climate⁴⁸. However, this approach treats environmental factors as a ‘black box’ to evaluate overall performance without isolating resistance to specific climatic extremes⁴⁸. (2) While wheat cultivars are assessed under different conditions, new cultivars are selected due to outstanding performance in favorable environments, where genetic variation and yield potential are greatest^{45,46}. This might deter gains in tolerance to stressful climates, where genotype and environment interactions are more pronounced^{17,45}. (3) The U.S. HWW breeding has largely focused on improving grain yield, biotic stresses, end-use quality, and

perhaps individual environmental stresses (e.g., drought stress)⁴⁹ rather than targeting combined abiotic stresses like HD⁴¹. For example, in central Kansas, wheat breeding programs have progressively targeted resistance to different diseases over the decades, focusing on stem rust during the 1970s, *Cephalosporium* stripe in the early 1980s, leaf-spotting fungi during the 1990s, and *Fusarium* head blight since the 2000s⁵⁰. However, climate change-oriented breeding remains a low priority, leading to failure to improve HD tolerance in most new cultivars⁵¹. (4) Genetic changes in modern wheat cultivars may have reduced HD resilience. The widespread adoption of semi-dwarf genes (*Rht1/Rht2*) during the Green Revolution increased yield potential by improving lodging resistance and allowing higher planting densities, particularly under favorable conditions⁵². However, these genes, gradually deployed after the 1960s and becoming dominant after 2000^{53,54}, also reduced root and coleoptile length, potentially limiting the ability of modern cultivars to access deeper soil moisture and thereby diminishing HD tolerance. Additionally, the 1RS translocation from rye to wheat was historically used to enhance drought tolerance by improving root systems, but it was gradually phased out in modern breeding programs due to the negative effects on wheat quality^{55,56}, possibly leading to reduced HD tolerance.

The second key finding is the variability in cultivar-specific response to HD, providing a basis for developing new, climate-resilient cultivars. The diversity in HD tolerance and yield potential among recently released cultivars also offers farmers a choice in selecting the most appropriate cultivars to plant in their fields based on climatic conditions. In areas frequently experiencing HD conditions, predominant in the western and southern portions of the U.S. Great Plains, farmers can prioritize cultivars with strong HD tolerance to mitigate yield losses and enhance yield stability. In contrast, those regions less affected by HD can benefit more from the cultivars with higher yield potential to optimize productivity in favorable environments.

Faced with increasing climate extremes in the future, our findings highlight the need for breeders to revisit their breeding objectives and strategies to enhance climate resilience, particularly HD resilience³⁵, without sacrificing productivity⁵⁷. Additionally, our results suggest that crop-climate modelers should consider cultivar-level adaptation to climate variability and extremes when predicting the risks of crop production failure. Our findings on cultivar-specific HD resilience further provide a basis for producer adaptation to climate change and underscore a new breeding target for improving future cultivars^{58,59}.

References

1. Wheeler, T. & Von Braun, J. Climate change impacts on global food security. *Science* **341**, 508-513 (2013).
2. Bentley, A. R. *et al.* Near-to long-term measures to stabilize global wheat supplies and food security. *Nat. Food* **3**, 483-486 (2022).
3. Xiong, W. *et al.* New wheat breeding paradigms for a warming climate. *Nat. Clim. Change* **14**, 869-875 (2024).
4. Zhang, L. *et al.* An unprecedented fall drought drives Dust Bowl-like losses associated with La Niña events in US wheat production. *Sci. Adv.* **10**, eado6864 (2024).
5. Lesk, C., Rowhani, P. & Ramankutty, N. Influence of extreme weather disasters on global crop production. *Nature* **529**, 84-87 (2016).
6. Tack, J., Barkley, A. & Nalley, L. L. Effect of warming temperatures on US wheat yields. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 6931-6936 (2015).
7. Lesk, C. *et al.* Compound heat and moisture extreme impacts on global crop yields under climate change. *Nat. Rev. Earth Environ.* **3**, 872-889 (2022).
8. Novick, K. A. *et al.* The increasing importance of atmospheric demand for ecosystem water and carbon fluxes. *Nat. Clim. Change* **6**, 1023-1027 (2016).
9. Zhao, H. *et al.* US winter wheat yield loss attributed to compound hot-dry-windy events. *Nat. Commun.* **13**, 1-9 (2022).
10. Field, C. B. *Managing the risks of extreme events and disasters to advance climate change adaptation: special report of the intergovernmental panel on climate change.* (Cambridge University Press, 2012).
11. Bailey-Serres, J., Parker, J. E., Ainsworth, E. A., Oldroyd, G. E. & Schroeder, J. I. Genetic strategies for improving crop yields. *Nature* **575**, 109-118 (2019).
12. Langridge, P., Braun, H., Hulke, B., Ober, E. & Prasanna, B. Breeding crops for climate resilience. *Theor. Appl. Genet.* **134**, 1607-1611 (2021).
13. Ober, E. S. *et al.* Wheat root systems as a breeding target for climate resilience. *Theor. Appl. Genet.* **134**, 1645-1662 (2021).
14. Cooper, M. & Messina, C. D. Breeding crops for drought-affected environments and improved climate resilience. *Plant Cell* **35**, 162-186 (2023).
15. Carpenter, S., Walker, B., Anderies, J. M. & Abel, N. From metaphor to measurement: resilience of what to what? *Ecosystems* **4**, 765-781 (2001).
16. Harfouche, A. L. *et al.* Accelerating climate resilient plant breeding by applying next-generation artificial intelligence. *Trends Biotechnol.* **37**, 1217-1235 (2019).
17. Xiong, W. *et al.* Increased ranking change in wheat breeding under climate change. *Nat. Plants* **7**, 1207-1212 (2021).
18. Kahiluoto, H. *et al.* Decline in climate resilience of European wheat. *Proc. Natl. Acad. Sci.*

- U.S.A.* **116**, 123-128 (2019).
19. Zhang, T. *et al.* Climate change may outpace current wheat breeding yield improvements in North America. *Nat. Commun.* **13**, 1-9 (2022).
 20. Shew, A. M., Tack, J. B., Nalley, L. L. & Chaminuka, P. Yield reduction under climate warming varies among wheat cultivars in South Africa. *Nat. Commun.* **11**, 1-9 (2020).
 21. Snowdon, R. J. *et al.* Reduced response diversity does not negatively impact wheat climate resilience. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 10623-10624 (2019).
 22. Braun, H.-J., Atlin, G. & Payne, T. Multi-location testing as a tool to identify plant response to global climate change. in *Climate Change and Crop Production* 115-138 (CABI Wallingford UK, 2010).
 23. Mittler, R. Abiotic stress, the field environment and stress combination. *Trends Plant Sci.* **11**, 15-19 (2006).
 24. Suzuki, N., Rivero, R. M., Shulaev, V., Blumwald, E. & Mittler, R. Abiotic and biotic stress combinations. *New Phytol.* **203**, 32-43 (2014).
 25. Tollenaar, M. & Lee, E. Yield potential, yield stability and stress tolerance in maize. *Field Crops Res.* **75**, 161-169 (2002).
 26. Rashid, M. A., Andersen, M. N., Wollenweber, B., Zhang, X. & Olesen, J. E. Acclimation to higher VPD and temperature minimized negative effects on assimilation and grain yield of wheat. *Agric. For. Meteorol.* **248**, 119-129 (2018).
 27. López, J., Way, D. A. & Sadok, W. Systemic effects of rising atmospheric vapor pressure deficit on plant physiology and productivity. *Glob. Change Biol.* **27**, 1704-1720 (2021).
 28. Vadez, V. *et al.* Crop traits and production under drought. *Nat. Rev. Earth Environ.* **5**, 211-225 (2024).
 29. Shimoda, S., Terasawa, Y. & Nishio, Z. Improving wheat productivity reveals an emerging yield gap associated with short-term change in atmospheric humidity. *Agri. For. Meteorol.* **312**, 108710 (2022).
 30. Monfreda, C., Ramankutty, N. & Foley, J. A. Farming the planet: 2. Geographic distribution of crop areas, yields, physiological types, and net primary production in the year 2000. *Glob. Biogeochem. Cycles* **22** (2008).
 31. Dupont, F. M. *et al.* Protein accumulation and composition in wheat grains: effects of mineral nutrients and high temperature. *Eur. J. Agron.* **25**, 96-107 (2006).
 32. Abatzoglou, J. T. Development of gridded surface meteorological data for ecological applications and modelling. *Int. J. Climatol.* **33**, 121-131 (2013).
 33. Nuttall, J. G., Barlow, K. M., Delahunty, A. J., Christy, B. P. & O'Leary, G. J. Acute high temperature response in wheat. *Agron. J.* **110**, 1296-1308 (2018).
 34. Jiang, T., He, L., Feng, H., He, J. & Yu, Q. Understanding the impacts of extreme temperature and humidity compounds on winter wheat traits in China. *Agric. For. Meteorol.* **362**, 110354 (2025).
 35. Barnabás, B., Jäger, K. & Fehér, A. The effect of drought and heat stress on reproductive

- processes in cereals. *Plant Cell Environ.* **31**, 11-38 (2008).
36. Wang, S., Zheng, H., Liu, S., Miao, Y. & Li, J. Numerical study on the stomatal responses to dry-hot wind episodes and its effects on land-atmosphere interactions. *Plos One* **11**, e0162852 (2016).
 37. Pinheiro, J. C. & Bates, D. M. *Linear mixed-effects models: basic concepts and examples*. (Springer-Verlag, New York, 2000).
 38. Cameron, A. C., Gelbach, J. B. & Miller, D. L. Robust inference with multiway clustering. *J. Bus. Econ. Stat.* **29**, 238-249 (2011).
 39. Wilks, D. S. *Statistical methods in the atmospheric sciences*. Vol. 100 (Academic press, 2011).
 40. Gelman, A. *Data analysis using regression and multilevel/hierarchical models*. (Cambridge university press, 2007).
 41. Graybosch, R., Baenziger, P., Hundera, F. & Dwiekat, I. Wheat breeding in the Great Plains of North America-Past, Present and Future. in *Using Cereal Science and Technology for the Benefit of Consumers* 39-43 (Elsevier, 2005).
 42. Lobell, D. B., Bänziger, M., Magorokosho, C. & Vivek, B. Nonlinear heat effects on African maize as evidenced by historical yield trials. *Nat. Clim. Change* **1**, 42-45 (2011).
 43. Long, S. P., Ainsworth, E. A., Leakey, A. D., Nosberger, J. & Ort, D. R. Food for thought: lower-than-expected crop yield stimulation with rising CO₂ concentrations. *Science* **312**, 1918-1921 (2006).
 44. Ziska, L. H. & Bunce, J. A. Predicting the impact of changing CO₂ on crop yields: some thoughts on food. *New Phytol.* **175**, 607-618 (2007).
 45. Assad, M. & Paulsen, G. Genetic changes in resistance to environmental stresses by US Great Plains wheat cultivars. *Euphytica* **128**, 85-96 (2002).
 46. Ceccarelli, S. Specific adaptation and breeding for marginal conditions. *Euphytica* **77**, 205-219 (1994).
 47. Tack, J., Barkley, A., Rife, T. W., Poland, J. A. & Nalley, L. L. Quantifying variety-specific heat resistance and the potential for adaptation to climate change. *Glob. Change Biol.* **22**, 2904-2912 (2016).
 48. Xiong, W., Reynolds, M. & Xu, Y. Climate change challenges plant breeding. *Curr. Opin. Plant Biol.* **70**, 102308 (2022).
 49. Grogan, S. M. *et al.* Phenotypic plasticity of winter wheat heading date and grain yield across the US Great Plains. *Crop Sci.* **56**, 2223-2236 (2016).
 50. Bockus, W. W. *et al.* Success stories: breeding for wheat disease resistance in Kansas. *Plant Dis.* **85**, 453-461 (2001).
 51. Kusunose, Y. *et al.* Sustaining productivity gains in the face of climate change: A research agenda for US wheat. *Glob. Change Biol.* **29**, 926-934 (2023).
 52. Graybosch, R. A. & Peterson, C. J. Genetic Improvement in Winter Wheat Yields in the Great Plains of North America, 1959-2008. *Crop Sci.* **50**, 1882-1890,

doi:10.2135/cropsci2009.11.0685 (2010).

53. Xu, Y. *et al.* Development and validation of diagnostic markers for the reduced height gene Rht8 in wheat. *Crop Sci.* **64**, 278-286 (2024).
54. Rebetzke, G. *et al.* Genotypic increases in coleoptile length improves stand establishment, vigour and grain yield of deep-sown wheat. *Field Crops Res.* **100**, 10-23 (2007).
55. Graybosch, R., Bai, G., Amand, P. S. & Sarath, G. Persistence of rye (*Secale cereale* L.) chromosome arm 1RS in wheat (*Triticum aestivum* L.) breeding programs of the Great Plains of North America. *Genet. Resour. Crop Evol.* **66**, 941-950 (2019).
56. Lelley, T., Eder, C. & Grausgruber, H. Influence of 1BL. 1RS wheat-rye chromosome translocation on genotype by environment interaction. *J. Cereal Sci.* **39**, 313-320 (2004).
57. Farooq, M., Bramley, H., Palta, J. A. & Siddique, K. H. Heat stress in wheat during reproductive and grain-filling phases. *Crit. Rev. Plant Sci.* **30**, 491-507 (2011).
58. Fleury, D., Jefferies, S., Kuchel, H. & Langridge, P. Genetic and genomic tools to improve drought tolerance in wheat. *J. Exp. Bot.* **61**, 3211-3222 (2010).
59. Langridge, P. & Reynolds, M. Breeding for drought and heat tolerance in wheat. *Theor. Appl. Genet.* **134**, 1753-1769 (2021).

Chapter 4 - A hidden role of phenological shifts in climate change impacts wheat yields

4.1. Introduction

Climate change poses severe challenges to the sustainable development of human society¹, with agriculture being among the most vulnerable sectors². Many studies have examined how climate variability and extremes affect crop yields³⁻⁶ and have concluded that inter-annual climate variability explains a large portion of year-to-year yield fluctuations³. In contrast, the role of long-term climate change in shaping yield trends has received relatively less attention, despite its importance in designing effective mitigation and adaptation strategies⁷. Several studies showed that rising temperature can substantially reduce yield at regional and global scales⁸⁻¹². However, most of these studies rely on static or fixed growing seasons^{8-10,12}. This assumption may lead to mis-interpretation of crop responses by overlooking the capacity of crops to naturally adjust their phenology under a changing climate.

Crop development is strongly temperature-dependent. Warmer conditions accelerate growth and advance key phenological stages such as heading and flowering¹³⁻¹⁷. These shifts can alter the duration of development phases and create mismatches between climatic extremes and sensitive growth stages, ultimately impacting yields¹⁷⁻²¹. For winter wheat, warming may positively or negatively influence winter wheat yield through direct temperature effects, such as reduced risk of cold injury and increased heat stress, and through indirect phenological shifts, including greater exposure to spring frosts^{22,23}, avoidance of heat stress, and changes in the duration of phenological phases^{24,25} (Figure 4.1). Accordingly, it is essential to account for both the timing and intensity of climate stresses throughout the growing season when assessing climate change impacts. Yet, isolating climate-driven phenological shifts is difficult because they often

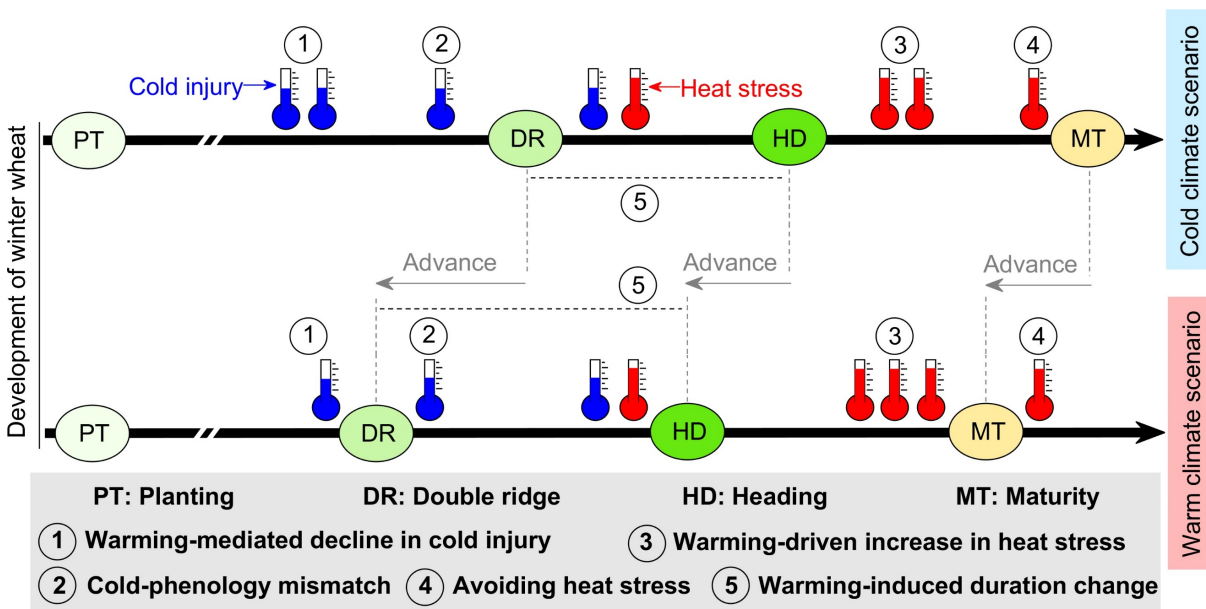


Figure 4.1. Schematic diagram illustrating the main effects of warming on winter wheat, accounting for phenological responses. Higher temperatures accelerate crop growth and development, advancing phenological stages and affecting yield primarily through five pathways.

relate to genetic factors. For a given cultivar, the thermal time required for development, also known as growing degree days (GDD), is generally constant^{13,17,26,27}. Rising temperatures do not change this requirement but advance phenological timing²⁵. Plant breeders, in turn, have gradually modified GDD requirements to maintain longer growth duration under a warming climate¹⁷, which makes it difficult to distinguish phenological changes driven by climate from those attributable to genetics¹³.

Ideally, the influence of climate change on phenology can be tracked by planting the same crop variety over multiple years across multiple sites. The U.S. Hard Winter Wheat Regional Nursery Program (HWWRNP) was established through collaboration between the U.S. Department of Agriculture (USDA) and multiple state agricultural experiment stations in the U.S. Great Plains. The program collected heading dates and yield data for multiple cultivars, consistently including the long-term check cultivar ‘Kharkof.’ Analysis of heading date trends at the long-term trial sites revealed consistent advances of 1-2 days per decade (Figure C.1). Since

Kharkof remained unchanged genetically, these shifts in heading date were mainly driven by climate change. This fixed-cultivar dataset therefore offers an opportunity to single out climate effects on yield trends under shifted phenological conditions^{13,28}.

Here, we developed a linear mixed-effects model to quantify the impacts of long-term climate change on winter wheat yields in the U.S. Great Plains from 1960 to 2024. We compared analyses based on observed phenological shifts with those assuming a fixed growing season as used in most prior studies. Finally, we decomposed the contributions of specific climate factors to climate-driven yield trends, providing a clearer understanding on how phenological shifts modulate the impacts of historical climate change on wheat yield trends.

4.2. Material and Methods

4.2.1 Data

Raw crop data, including observed yields and heading dates for the hard winter wheat cultivar Kharkof, were obtained from the USDA-Agricultural Research Service (ARS), Hard Winter Wheat Regional Performance Nursery, where Kharkof has served as the long-term check in all field trials²⁹. We extracted dryland site-years with records of both heading date and yield from 1960 to 2024 across 13 states (North Dakota, Montana, Minnesota, South Dakota, Wyoming, Iowa, Nebraska, Colorado, Kansas, Missouri, Oklahoma, New Mexico, and Texas), representing 71% of U.S. winter wheat area (Figure C.1; Table C.1).

Daily maximum temperature, minimum temperature, and precipitation from 1960 to 2024 were obtained from the Daily U.S. Climate Gridded Dataset (NClimGrid-daily), a 5-km resolution gridded product maintained by the National Oceanic and Atmospheric Administration (NOAA; Table C.1). For each site, we derived climate data by averaging values from the five nearest

NClimGrid-daily grid points.

4.2.2 Phenology

Heading dates were recorded as the wheat growing stage when 50% of plants had fully emerged spikes from the flag leaf. The observed heading dates were then used to estimate two key phenological stages: double ridge (DR) and maturity (MT)¹⁸. The DR stage marks the onset of reproductive development and floral initiation, whereas the HD stage represents the completion of spike development and the transition toward anthesis. During the DR-HD period, the terminal spikelet forms, determining the total number of spikelets per spike. The HD-MT period encompasses grain set and grain filling, ultimately determining grain weight. Since temperature mainly affects the duration of developmental phases, a practical approach to estimate approximate MT and DR is through thermal time, also known as growing degree days (GDD, °C days)^{21,22,30-33}. Using this approach, MT for each site-year was defined as the calendar date when cumulative GDD since HD reached 718 °C days²² (GDD_{HD-MT}). Although this value represents a generic dryland threshold for the U.S. Great Plains rather than a Kharkof-specific threshold, validation against the 79 available observed MT dates across a broad spatial range (Figure C.2) showed strong agreement, with a root mean square error (RMSE) of only 3 days (Figure C.3). We also tested an alternative threshold of GDD_{HD-MT} (800 °C days), previously applied to Kharkof in Bushland, Texas²¹, but this reduced accuracy in our study domain (RMSE = 5 days). Thus, we applied the 718 °C days for GDD_{HD-MT} to estimate MT for all site-years (Figure C.4). A similar approach was used to infer DR, based on a cumulative GDD_{DR-HD} of 549 °C days from DR to HD²² (Figure C.4). The detailed calculation of GDD was provided in Supplementary Text C.1. Planting date (PT) data were available for only 181 site-years in our dataset. To obtain representative PT for each site, we

included additional PT data (3,071 observations) from dryland Variety Test Reports across the 13 states (1960-2024) in this study (Table C.1). After excluding those sites with fewer than two years of records, 296 sites (3,131 observations; Figure C.5a) remained, and the mean PT was calculated for each site. These averages were then spatially interpolated to our study sites (Figure C.5b).

4.2.3 Regression Model

To ensure reliable estimation, we excluded sites with fewer than 3 years of trial data, remaining 1,101 observations across 58 sites (Figure 4.2a), and then quantified the impact of climate variables on yields using the following linear mixed-effects model³⁴:

$$Y_{l,t} = \alpha_l + \beta_{0,state} year_t + f(W_{l,t}; \beta_{var}) + \varepsilon_{l,t} \quad (1)$$

$$f(W_{l,t}; \beta_{var}) = \sum_{p=1}^2 \beta_{1,p} FDD_{l,t,p} + \sum_{p=2}^3 \beta_{2,p} EDD_{l,t,p} + \sum_{p=1}^3 \beta_{3,p} Prcp_{l,t,p} + \sum_{p=1}^3 \beta_{4,p} Prcp_{l,t,p}^2 + \beta_5 P1_{l,t} + \beta_6 P2_{l,t} + \beta_7 P3_{l,t} \quad (2)$$

where $Y_{l,t}$ is the yield of Kharkof at location “ l ” in year “ t ”. α_l is the location-specific random effect that accounts for time-invariant spatial heterogeneity such as soil properties. $\beta_{0,state}$ captures the state-specific linear time trend, reflecting changes in management practices over time. $f(W_{l,t}; \beta_{var})$ represents the effects of specific variables with their corresponding coefficients β . The error term $\varepsilon_{l,t}$ is likely heteroskedastic and autocorrelated. Therefore, we clustered standard errors (SEs) by locations, which accounts for autocorrelation in coefficient estimation. The adjusted SEs enabled the production of more conservative p-values (Table C.2).

For the climate variables in Eq. 2, we included climate indices such as freezing degree days (FDD , °C days), extreme degree days (EDD , °C days) (Supplementary Text C.1), and both linear and quadratic terms for total precipitation ($Prcp$, mm) during specific phenological periods ($p = 1$,

2, and 3 for PT-DR, DR-HD, and HD-MT, respectively). To reduce the degrees of freedom, the FDD_{p3} and EDD_{p1} were not included in our model due to their uncommon occurrence in actual climate conditions³⁵. Additionally, we included the lengths of three phenological periods (P1, P2, and P3) as explanatory variables. These lengths affected yield, and for a given cultivar (i.e., Kharkof), their variations were largely temperature-driven, particularly for P2 and P3. Thus, we treated them as climate variables. Finally, we assessed multicollinearity among all variables using the variance inflation factor (VIF)³⁶. The VIF values less than 3 for all variables indicated no serious multicollinearity problem in the model.

4.2.4 Quantifying the impact of climate trends

Among all sites, 12 long-term trial sites [34.3°N-48.1°N] had observed HD records for at least 30 years, with the observation periods spanning more than 50 years (Figure C.1). Despite these long-term records, the amount of missing data varied across the 12 sites (Figure C.1). To enable fair comparisons of yield impacts driven by climate trends among sites, we gap-filled HD for missing years. Specifically, for each site, we estimated HD for missing years by applying the mean cumulative GDD from January 1^{22,31,32} to the observed HD ($GDD_{1/1-HD}$) across all available years at that site as the threshold. Validation against observed records showed RMSE of 5 days across the 12 sites (Figure C.6), confirming the method's reliability. Based on the completed HD dates (Figure C.7), we then inferred the other phenological stages (PT, DR, and MT; Figure C.8) using the previous approach described above.

Next, we quantified the impact of climate trends using a three-step process¹⁰:

(1) Notation:

$Cli_{l,t}$ = all observed climate variables used in Eq. 2 for location “ l ” in year “ t ”

$Cli'_{l,t}$ = predicted climate variables, based on a linear fit for 1960-2024

$Cli^d_{l,t}$ = detrended climate variables = $Cli_{l,t} - Cli'_{l,t} + Cli'_{l,1960}$

(2) Model predictions (Eq. 1; f):

$f(Cli_{l,t})$ = predicted yields using observed climate variables

$f(Cli^d_{l,t})$ = predicted yields using detrended climate variables

(3) The yield effect of climate trends was quantified as the temporal trend of $[f(Cli_{l,t}) - f(Cli^d_{l,t})]$.

Finally, we assessed the uncertainty in climate trend impacts by constructing the 95% confidence intervals (2.5th-97.5th percentiles) from 1,000 bootstrap resamples, in which historical data were resampled, and the three-step procedure was repeated for each sample.

Additionally, we quantified the yield effect of trends on individual climate variables by replacing $Cli^d_{l,t}$ in steps (2) and (3) with detrended values for the specific variables of interest, while keeping all other variables at their observed values.

4.3. Results

4.3.1 The impacts of climate trends on yields

Using a lineal mixed-effects model with 1,101 yield observations for Kharkof (Figure 4.2a), we first quantified yield responses to multiple climate variables, including crop-related climate indices (freezing degree days (FDD), extreme degree days (EDD), and cumulative precipitation) during specific phenological phases, as well as changes in the durations of the phenological phases (Methods). The model showed that increases in FDD and EDD reduced yield, and yield responses to precipitation followed a concave, nonlinear pattern across three phenological phases, with both drought and excessive rainfall lowering yields (Table C.2).

Additionally, the model showed that yield increased with longer DR-HD and HD-MT phases (Table C.2).

We applied the regression analysis of historical data to estimate the impacts of climate trends on grain yield at 12 long-term trial sites from 1960 to 2024 (Figure 4.2a; Methods). The results revealed a latitudinal gradient, shifting from positive impacts in the north to negative in the south of the Great Plains (red line in Figure 4.2b). Based on latitude, sites were grouped into three regions: north ($> 42^{\circ}\text{N}$), central (38°N - 42°N), and south ($< 38^{\circ}\text{N}$). In the north region, climate

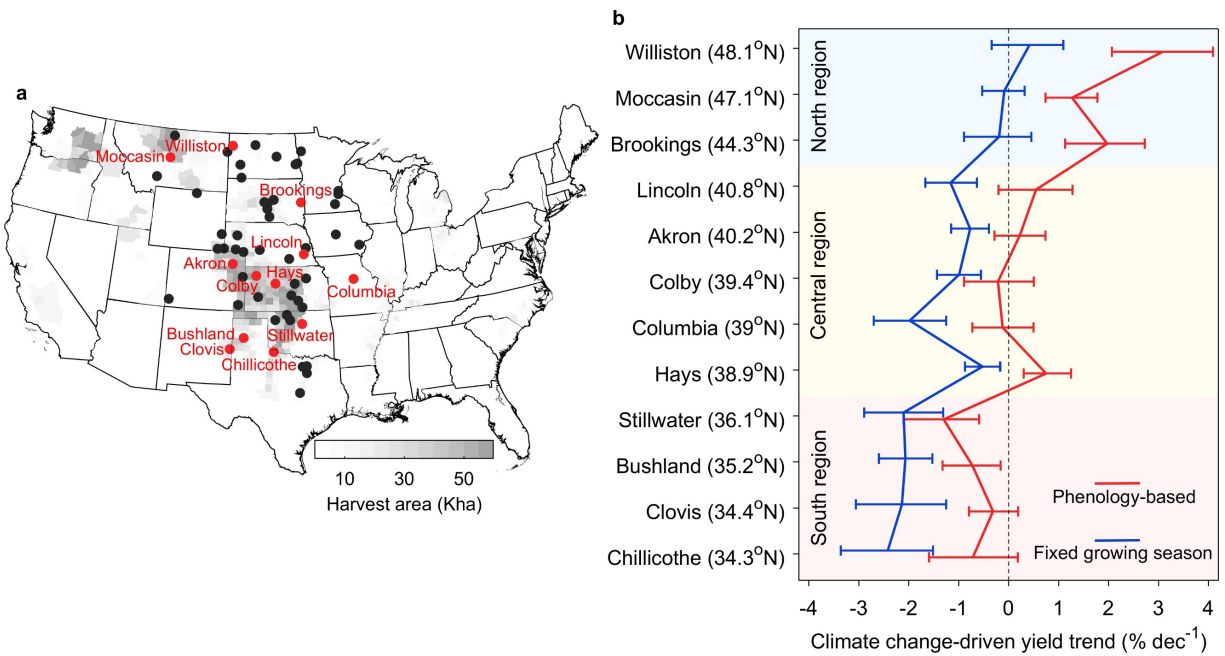


Figure 4.2. Climate change-driven yield trends from 1960 to 2024 estimated using two approaches. a, Map of trial sites included in our model (black and red dots) and the 12 long-term trial sites used for climate impact analysis (red dots). Background shading represents the county-level average harvested area of winter wheat in the U.S. during 2001-2020, based on USDA-NASS data. b, Estimated climate change-driven yield trends for the 12 long-term sites using phenology-based (red) and fixed growing season (blue) approaches. Values are expressed as a percentage of the average yield in our samples (2.3 t ha^{-1}). Error bars show the 2.5th-97.5th percentiles from 1,000 bootstrap replicates. Based on latitude, the 12 locations were grouped into three regions: north, central, and south regions, indicated by blue, yellow, and red background shading, respectively.

trends significantly ($p\text{-value} < 0.05$) increased yield, with average yield gains of $2.1\% \text{ dec}^{-1}$ ($1.3\% \text{ dec}^{-1}$, $2.0\% \text{ dec}^{-1}$, and $3.1\% \text{ dec}^{-1}$ for Moccasin, Brookings, and Williston, respectively) relative to

the sample average (2.3 t ha^{-1}) (red line in Figure 4.2b). In the central region, most sites showed insignificant yield impacts (red line in Figure 4.2b). In the south region, Stillwater ($-1.3\% \text{ dec}^{-1}$) and Bushland ($-0.7\% \text{ dec}^{-1}$) experienced significant ($p\text{-value} < 0.05$) yield declines, whereas Clovis and Chillicothe showed insignificant yield effects (red line in Figure 4.2b).

By contrast, when we used a fixed-season approach to evaluate climate change-driven yield trends, we assumed an unchanging growing season over time and incorporated climate variables as nonlinear functions of average temperature and cumulative precipitation during this fixed period (Supplementary Text C.2 and Table C.3). Although the latitudinal gradient in climate impacts was similar, this approach consistently overestimated negative impacts of climate change across all sites (blue line in Figure 4.2b). Specifically, this approach detected no significant effects in the north region, but significant negative effects ($p\text{-value} < 0.05$) in the central and south regions, with the strongest impact of $-2.4\% \text{ dec}^{-1}$ at the southernmost site (Chillicothe), approximately three times larger than the phenology-based estimate ($-0.7\% \text{ dec}^{-1}$; Figure 4.2b).

4.3.2 Disentangling climate trend impacts by specific variables

We further decomposed the total climate-driven yield trend (red line in Figure 4.2b) into contributions from individual variables (Figure 4.3). Across all three regions, extension of the DR-HD phase made a relatively large positive contribution to yield trends (Figure 4.3). Winter warming, reflected in a mean temperature increase of $0.34 \text{ }^{\circ}\text{C dec}^{-1}$ ($p\text{-value} < 0.05$; Figure 4.4a), significantly advanced the DR stage by $1.8 \text{ days dec}^{-1}$ ($p\text{-value} < 0.05$; Figure 4.4b). The earlier DR stage, combined with higher spring temperatures¹³ ($0.18 \text{ }^{\circ}\text{C dec}^{-1}$; $p\text{-value} < 0.05$; Figure 4.4c), further advanced HD by $1.2 \text{ days dec}^{-1}$ ($p\text{-value} < 0.05$; Figure 4.4d). These shifts exposed crop development to cooler conditions, with mean temperatures during the DR-HD phase significantly

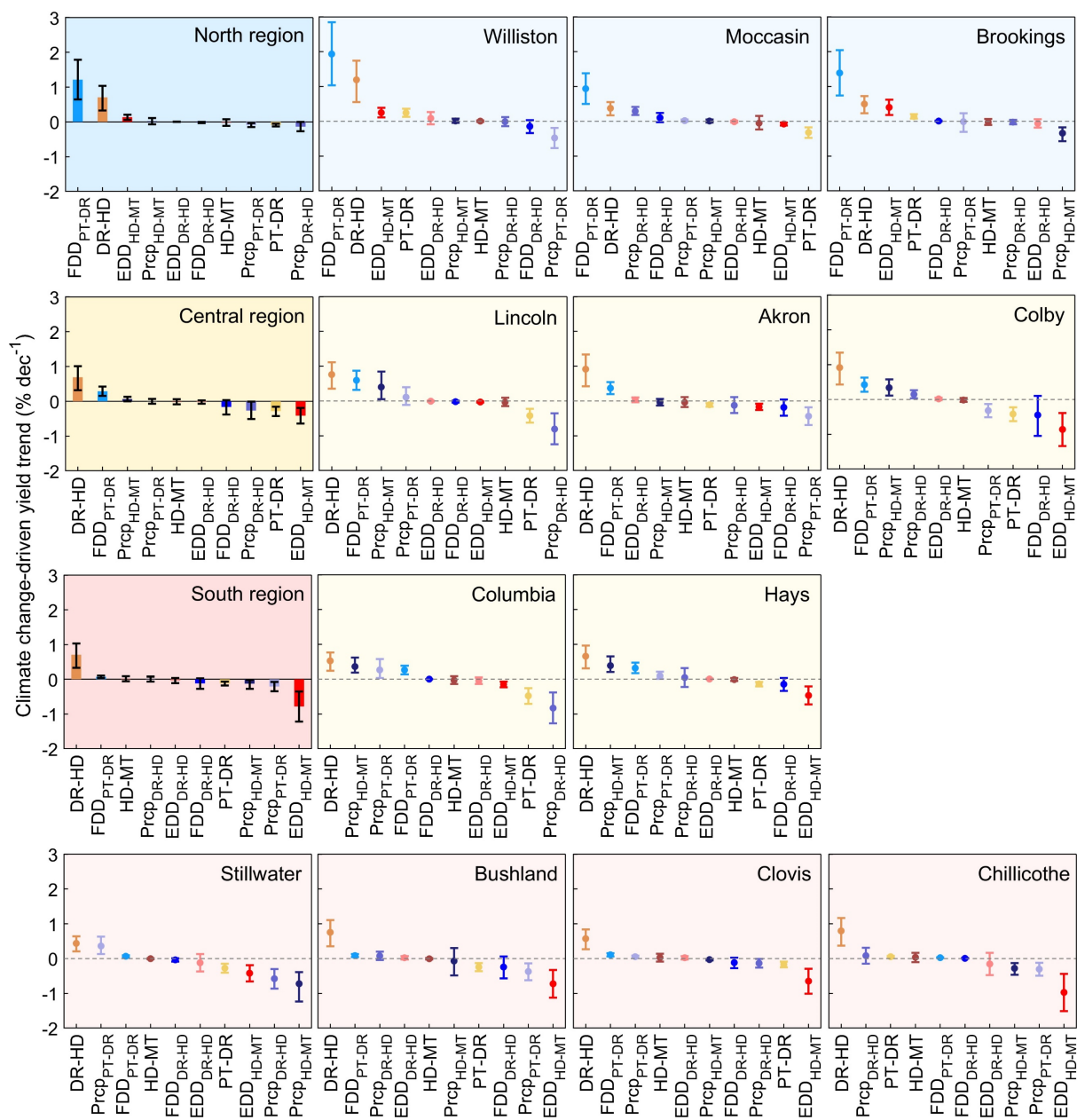


Figure 4.3. Disentangling climate trend impacts from 1960 to 2024. Climate change-driven yield trends were separated by individual climate variables, including freezing degree days (FDD), extreme degree days (EDD), and cumulative precipitation (Prcp) during specific phenological phases and phases durations (planting to double ridge, PT-DR; double ridge to heading, DR-HD; and heading to maturity, HD-MT) for each site (light background shading). Regional averages for the north (blue), central (yellow), and south (red) regions are shown with dark background shading, and site panels are shaded to match their respective regions. Mean estimates are represented by color-coded bars in the regional panels and by color-coded dots in the site panels. Values are expressed as a percentage of the average yield in our samples (2.3 t ha⁻¹). Error bars indicate the 2.5th-97.5th percentiles from 1,000 bootstrap replicates.

declining by $-0.24\text{ }^{\circ}\text{C dec}^{-1}$ (p-value < 0.05; Figure 4.4e). Since the thermal time (GDD) required

between the stages is relatively fixed for a given cultivar, particularly after vernalization is satisfied^{31,32}, this cooler temperature prolonged the DR-HD phase by 0.6 days dec⁻¹ (p-value <

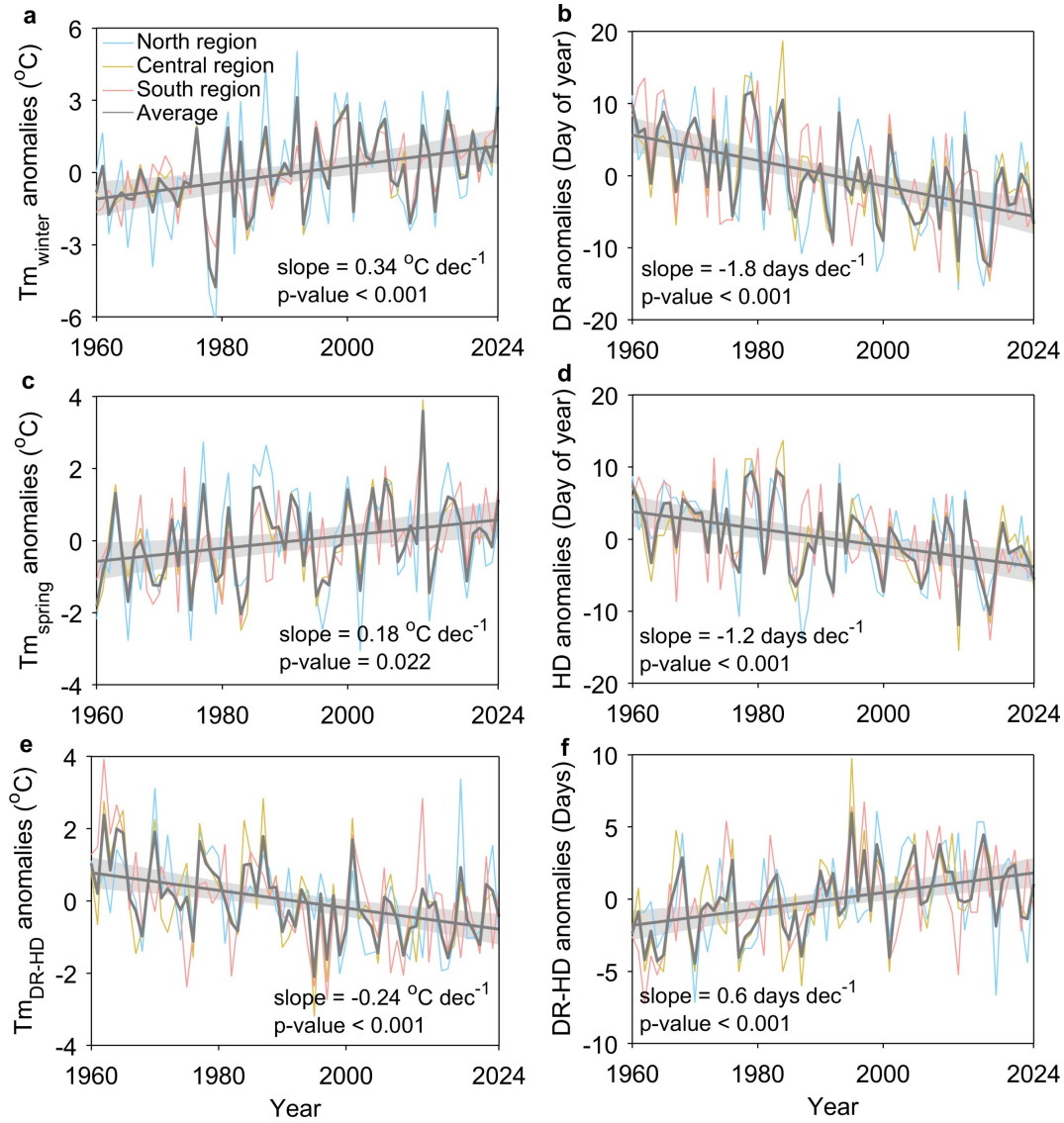


Figure 4.4. Time series in temperature and phenology anomalies from 1960 to 2024. a, Mean temperature (Tm) during winter (December-February). b, Double ridge (DR) dates. c, Tm during spring (March-May). d, Heading (HD) dates. e, Tm during the DR-HD phase. f, Duration of the DR-HD phase. Anomalies were first calculated relative to the 1960-2024 average for each site, and then averaged across sites within each region: north (blue), central (yellow), and south (red). Gray lines show the overall average across all sites and the linear regression trends based on the Mann-Kendall test, with gray shading representing the 95% confidence intervals.

0.05; Figure 4.4f). The extensions of the DR-HD phase across regions due to temperature increase thus produced consistently positive contributions to yield trends (Figure 4.3 and Figure C.9). By

contrast, although the HD stage occurred earlier under warming, higher temperatures during the grain filling period accelerated development, offsetting the potential extension of this phase. As a result, the HD-MT duration showed no significant long-term change (Figure C.10) and therefore did not contribute noticeably to yield trends (Figure 4.3).

Regionally, winter warming provided particularly large benefits in the north, where cold injury occurs more frequently due to lower temperatures³⁷. A reduction in FDD during the PT-DR phase further enhanced yield trends in this region (Figure 4.3). In the central region, however, warming increased EDD during the HD-MT phase, partially offsetting the benefits from the longer DR-HD phase. In the south region, even larger increases in EDD during the HD-MT phase led to greater yield reductions (Figure 4.3), suggesting that the negative effects of higher temperatures during this period outweighed the advantages of heat escape through earlier maturity (Figure C.8). The contributions of individual climate variables also varied across sites (Figure 4.3).

We also decomposed the climate-driven yield trend estimated by the fixed-season approach (blue line in Figure 4.2b) into the contributions from temperature and precipitation (Supplementary Text C.2). Here, negative impacts were primarily driven by temperature trends (Figure C.11a), consistent with previous findings¹⁰. For example, in the south region, rising temperatures reduced yields by 1.7% dec⁻¹ (p-value < 0.05; Figure C.11a). In contrast, the phenology-based framework partitioned temperature impacts into EDD, FDD, and temperature-driven changes in phenological duration, providing a more nuanced assessment. Similarly, the impacts of precipitation trends were estimated by summing contributions across all three phenological phases, confirming that precipitation trends were not the main driver of climate impacts. Importantly, we found that temperature trends did not significantly reduce yields in the central and south regions and even contributed positively to yield gains of 2.3% dec⁻¹ in the north region (Figure C.11b). This

discrepancy highlights that fixed-season approach overestimates the negative effects of warming.

4.4. Discussion

The evaluation of climate change-driven yield trends may be subject to several limitations. First, due to the limited records of planting date in the Kharkof dataset, we estimated the average planting date for each site based on dryland Variety Test Reports, which documented observed planting dates across the U.S. Great Plains (Methods; Table C.1). While this approach may not fully capture interannual climate variability during the PT-DR phase, its effect on our model estimates is likely minimal. This is because the primary climate stresses affecting yield, such as cold injury, spring frost, and heat stress, typically occur after the later vegetative stage (Figure 4.1), making long-term trends in these climate variables largely unaffected. Additionally, winter wheat is generally fully vernalized by the time when dormancy ends and resumes growth in early spring, implying that planting date has limited influence on phenological timing once vernalization requirements are satisfied^{13,25}. Finally, planting date adjustments often reflect management decisions, whereas our study aims to isolate climate-driven phenological shifts. Therefore, adopting a fixed PT date provides a consistent framework for assessing long-term climate impacts on yield.

Second, MT dates can be directly inferred from observed heading dates using thermal time without accounting for photoperiod effects^{38,39} (Figure C.3). Ideally, the thermal time between DR and HD should be adjusted based on cultivar-specific photoperiod sensitivity³⁹. However, because the datasets on the photoperiod sensitivity of Kharkof and its DR dates are unavailable, we could not explicitly determine DR timing. Instead, we adopted reported GDD value for the DR-HD phase without photoperiod adjustment, which have been widely applied to estimate winter wheat

phenology in the U.S. Great Plains^{22,35} (Methods). Although this approach may introduce some systematic bias in estimating DR dates, it is unlikely to affect long-term trend estimation for DR-HD. Nevertheless, more detailed observed phenological data would help further refine stage-specific estimates and improve the accuracy of future climate impact assessments.

Third, isolating the effects of cultivar changes is critical for estimating long-term climate change impacts. To address this, we used Kharkof, a hard red winter wheat cultivar introduced to the United States in the early 20th century⁴⁰, as a fixed reference cultivar, since it was the only check cultivar consistently included across all sites and years in our dataset. Changes in heading dates of Kharkof were primarily attributable to temperature change, but it is also reasonable to consider whether seeding rates or other management factors, such as fertilizer application, may have influenced the heading dates. As noted by Geleta et al. (2002), reasonable seeding rates affect heading dates by only ± 1 day⁴¹, indicating that long-term changes in seeding rates had no noticeable net effect¹³. Fertilizer applications could potentially delay heading by stimulating additional tillers; therefore, improved soil fertility in recent decades would not explain the earlier heading observed¹³. Although the inclusion of additional check cultivars could provide a more comprehensive assessment, it is not possible to reconstruct historical conditions or expose modern cultivars to past climates consistently. Importantly, this study emphasizes that accounting for phenological shifts is essential for accurately capturing the true effects of long-term climate change on crop yields.

Lastly, elevated atmospheric CO₂ is expected to enhance wheat yield through fertilization effects and improved water-use efficiency⁴². While our analysis does not explicitly account for the yield effect of elevated CO₂, this additional CO₂ fertilization benefit may further amplify the positive yield trends associated with climate change.

Research on long-term climate impacts has generally relied on two approaches: process-based crop models and statistical models⁴³. Crop models can simulate crop growth and phenological responses under varying environments, but their reliance on high-quality input data on crop management, growth, and soil conditions limits their large-scale applicability⁴⁴. In the absence of cultivar-specific yield observations, simulated yields from crop models (i.e., DSSAT) have been used to estimate long-term climate impacts; however, research indicated such models may overstate the influence of rainfall trends due to their high sensitivity to water stress⁴³. By contrast, statistical models are more practical for large-scale studies because they do not rely on detailed field or management inputs⁴⁴. Instead, they typically account for spatial and temporal variability (i.e., soil conditions and management practices) through site and year effects, which has made them widely applied in climate-yield assessments^{10,45}. Nonetheless, most statistical analyses for long-term climate change impacts have relied on static crop calendars^{8-10,12}. While sufficient for quantifying the effects of climate variability and extreme events, this approach can bias estimates of long-term trends, since warming alters crop growth and development, enabling gradual phenological adaptation over time. In this study, based on observed phenological data, we provide evidence of this adaptive benefit, showing that an extended double ridge to heading phase primarily mitigates the effects of heat stress during the grain filling period. This occurs because late-winter warming shortens the overwintering period, advances regreening, and extends the subsequent active growth periods, favoring spikelet development and ultimately increasing kernel number per spike^{28,46}.

4.5. Conclusion

In summary, this study evaluated how historical climate trends have affected winter wheat

yields across the U.S. Great Plains over the past 65 years (1960-2024). To our knowledge, it provides the first evidence of the long-term climate fingerprint on U.S. winter wheat yields under changing phenology, using a fixed-cultivar dataset. We found that long-term climate trends did not markedly reduce yields and even contributed positively in the northern region. Our phenology-based framework revealed that warming can induce natural crop adaptation through shifts in developmental timing, particularly by extending the DR-HD phase, which partially offsets the adverse effects of rising temperatures. Importantly, without accounting for phenological shifts and phase-specific climate conditions, assessments of long-term climate impacts would overstate the negative effects by roughly threefold, largely due to overestimation of temperature-driven impacts.

These findings deepen our understanding of how climate change influences crop yields and highlight the importance of incorporating phenological changes into long-term climate impacts assessments. Our results also suggest that targeted breeding and management strategies, such as optimizing the timing of spike differentiation or aligning cultivar selection with local climate trajectories, could enhance adaptation to future warming.

References

1. Stocker, T. et al. (eds) *Climate Change 2013: The Physical Science Basis: Working Group I Contribution To The Fifth Assessment Report Of The Intergovernmental Panel On Climate Change* (Cambridge Univ. Press, 2014).
2. Motha, R. P. & Baier, W. Impacts of present and future climate change and climate variability on agriculture in the temperate regions: North America. *Clim. Change* **70**, 137-164 (2005).
3. Ray, D. K., Gerber, J. S., MacDonald, G. K. & West, P. C. Climate variation explains a third of global crop yield variability. *Nat. Commun.* **6**, 5989 (2015).
4. Lesk, C., Rowhani, P. & Ramankutty, N. Influence of extreme weather disasters on global crop production. *Nature* **529**, 84-87 (2016).
5. Auffhammer, M. & Schlenker, W. Empirical studies on agricultural impacts and adaptation. *Energy Econ.* **46**, 555-561 (2014).
6. Zhang, L. *et al.* An unprecedented fall drought drives Dust Bowl-like losses associated with La Niña events in US wheat production. *Sci. Adv.* **10**, eado6864 (2024).
7. Lobell, D. B. & Di Tommaso, S. A half-century of climate change in major agricultural regions: Trends, impacts, and surprises. *Proc. Natl. Acad. Sci. U.S.A.* **122**, e2502789122 (2025).
8. Moore, F. C. & Lobell, D. B. The fingerprint of climate trends on European crop yields. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 2670-2675 (2015).
9. Kukal, M. S. & Irmak, S. Climate-driven crop yield and yield variability and climate change impacts on the US Great Plains agricultural production. *Sci. Rep.* **8**, 1-18 (2018).
10. Lobell, D. B., Schlenker, W. & Costa-Roberts, J. Climate trends and global crop production since 1980. *Science* **333**, 616-620 (2011).
11. Kucharik, C. J. & Serbin, S. P. Impacts of recent climate change on Wisconsin corn and soybean yield trends. *Environ. Res. Lett.* **3**, 034003 (2008).
12. Wang, Z., Ye, T., Wang, J., Cheng, Z. & Shi, P. Contribution of climatic and technological factors to crop yield: empirical evidence from late paddy rice in Hunan Province, China. *Stoch. Environ. Res. Risk Assess.* **30**, 2019-2030 (2016).
13. Hu, Q., Weiss, A., Feng, S. & Baenziger, P. S. Earlier winter wheat heading dates and warmer spring in the US Great Plains. *Agric. For. Meteorol.* **135**, 284-290 (2005).
14. Chmielewski, F.-M., Müller, A. & Bruns, E. Climate changes and trends in phenology of fruit trees and field crops in Germany, 1961–2000. *Agric. For. Meteorol.* **121**, 69-78 (2004).
15. Menzel, A. *et al.* European phenological response to climate change matches the warming pattern. *Glob. Change Biol.* **12**, 1969-1976 (2006).
16. Estrella, N., Sparks, T. H. & Menzel, A. Trends and temperature response in the phenology of crops in Germany. *Glob. Change Biol.* **13**, 1737-1747 (2007).
17. Fatima, Z. *et al.* The fingerprints of climate warming on cereal crops phenology and adaptation options. *Sci. Rep.* **10**, 18013 (2020).

18. Acevedo, E., Silva, P. & Silva, H. Wheat growth and physiology. *Bread wheat, improvement and production* **30**, 39-70 (2002).
19. Asseng, S. *et al.* Rising temperatures reduce global wheat production. *Nat. Clim. Change* **5**, 143-147 (2015).
20. Minoli, S., Jägermeyr, J., Asseng, S., Urfels, A. & Müller, C. Global crop yields can be lifted by timely adaptation of growing periods to climate change. *Nat. Commun.* **13**, 7079 (2022).
21. Shrestha, R. *et al.* Winter wheat response to climate change under irrigated and dryland conditions in the US southern High Plains. *J. Soil Water Conserv.* **75**, 112-122 (2020).
22. Li, X. *et al.* Wheat plants exposed to winter warming are more susceptible to low temperature stress in the spring. *Plant Growth Regul.* **77**, 11-19 (2015).
23. Moriondo, M. & Bindi, M. Impact of climate change on the phenology of typical Mediterranean crops. *Ital. J. Agrometeorol* **3**, 5-12 (2007).
24. Yu, H. *et al.* The effects of phased warming during late winter and early spring on grain yield and quality of winter wheat (*Triticum aestivum* L.). *Agronomy* **13**, 1909 (2023).
25. Asseng, S., Foster, I. & Turner, N. C. The impact of temperature variability on wheat yields. *Glob. Change Biol.* **17**, 997-1012 (2011).
26. Peairs, F. B. *Wheat Production and Pest Management for the Great Plains Region*. (Colorado State University Extension, 2010).
27. Butler, E. E. & Huybers, P. Variations in the sensitivity of US maize yield to extreme temperatures by region and growth phase. *Environ. Res. Lett.* **10**, 034009 (2015).
28. Stewart, B. A., Thapa, S., Xue, Q. & Shrestha, R. Climate change effect on winter wheat (*Triticum aestivum* L.) yields in the US Great Plains. *J. Soil Water Conserv.* **73**, 601-609 (2018).
29. Reitz, L. P. & Salmon, S. C. *Hard red winter wheat improvement in the plains: a 20-year summary*. (US Department of Agriculture, 1959).
30. McMaster, G. S. & Wilhelm, W. Growing degree-days: one equation, two interpretations. *Agric. For. Meteorol.* **87**, 291-300 (1997).
31. McMaster, G. S. *et al.* PhenologyMMS: A program to simulate crop phenological responses to water stress. *Comput. Electron. Agric.* **77**, 118-125 (2011).
32. McMaster, G. S., Wilhelm, W. & Frank, A. Developmental sequences for simulating crop phenology for water-limiting conditions. *Aust. J. Agric. Res.* **56**, 1277-1288 (2005).
33. Woli, P., Xue, Q., Smith, G. R., Long, C. R. & Rouquette Jr, F. M. Estimating the Drought-Induced Yield Loss for Winter Wheat in a Semi-Arid Region of the Southern United States Using a Drought Index. *Agric. Sci.* **15**, 812-829 (2024).
34. Pinheiro, J. C. & Bates, D. M. Linear mixed-effects models: basic concepts and examples. *Mixed-effects models in S and S-Plus*, 3-56 (2000).
35. Zhao, H. *et al.* US winter wheat yield loss attributed to compound hot-dry-windy events. *Nat. Commun.* **13**, 7233 (2022).

36. Wilks, D. S. *Statistical methods in the atmospheric sciences*. Vol. 100 (Academic press, 2011).
37. Zhu, P. *et al.* The critical benefits of snowpack insulation and snowmelt for winter wheat productivity. *Nat. Clim. Change* **12**, 485-490 (2022).
38. Cao, W. & Moss, D. Modelling phasic development in wheat: a conceptual integration of physiological components. *J. Agric. Sci.* **129**, 163-172 (1997).
39. Weir, A. H., Bragg, P., Porter, J. & Rayner, J. A winter wheat crop simulation model without water or nutrient limitations. *J. Agric. Sci.* **102**, 371-382 (1984).
40. Woli, P., Smith, G. R., Long, C. R. & Rouquette Jr, F. M. Predicting the Yield Loss of Winter Wheat Due to Drought in the Llano Estacado Region of the United States Based on the Cultivar-Specific Sensitivity to Drought. *Agric. Sci.* **16**, 13-30 (2025).
41. Geleta, B. *et al.* Seeding rate and genotype effect on agronomic performance and end - use quality of winter wheat. *Crop Sci.* **42**, 827-832 (2002).
42. Long, S. P., Ainsworth, E. A., Leakey, A. D., Nosberger, J. & Ort, D. R. Food for thought: lower-than-expected crop yield stimulation with rising CO₂ concentrations. *Science* **312**, 1918-1921 (2006).
43. Maltais-Landry, G. & Lobell, D. B. Evaluating the contribution of weather to maize and wheat yield trends in 12 US counties. *Agron. J.* **104**, 301-311 (2012).
44. Shi, W., Tao, F. & Zhang, Z. A review on statistical models for identifying climate contributions to crop yields. *J. Geogr. Sci.* **23**, 567-576 (2013).
45. Schlenker, W. & Roberts, M. J. Nonlinear temperature effects indicate severe damages to US crop yields under climate change. *Proc. Natl. Acad. Sci. U.S.A.* **106**, 15594-15598 (2009).
46. Fan, Y. *et al.* Winter night warming improves pre-anthesis crop growth and post-anthesis photosynthesis involved in grain yield of winter wheat (*Triticum aestivum* L.). *Field Crops Res.* **178**, 100-108 (2015).

Appendix A - Supplemental Information for Chapter 2

Text A.1. Conceptual framework

Crop production (P) is defined as the product of yield (Y) and harvested area (HA). HA can be further expressed as the product of planted area (PA) and harvestable fraction ($\frac{HA}{PA}$). A proportion of PA may be abandoned ($f_{ab} = \frac{PA-HA}{PA}$). Final county-level production can be calculated as:

$$P = \frac{HA}{PA} \times PA \times Y = (1 - f_{ab}) \times PA \times Y \quad [S1]$$

Given the marginal relationship between pre-season fall precipitation and planted area (Figure A.12), we assume that weather conditions during both wheat pre-season and in-season do not impact planted areas. It seems evident that climate conditions have little bearing on farmers' planting decisions in Kansas. Instead, planting decisions are more likely guided by non-environmental influences (i.e., long-term agricultural strategies, socio-economic factors, and policy incentives). Thus, in this study, both pre-season and in-season climate conditions affect production variability presumably through crop abandonment and yield variations. To estimate the impacts of climate-induced changes in abandonment and yields on total production across the Dust Bowl decade (1931-1940), the latest decade (2013-2022), and year 2023, we decomposed actual production [S1] into three components: expected base production (P_{base}), changes in production due to abandonment (ΔP_{fab}), and changes in production due to reductions in per-acre-harvested yield (ΔP_Y).

We firstly substituted yields (Y) with the sum of expected base yields (Y_{base}) and yield anomalies (ΔY) in equation [S1], and introduced the terms of abandonment in normal years ($\overline{f_{ab}}$), resulting in the following:

$$P = (1 - f_{ab} + \overline{f_{ab}} - \overline{f_{ab}}) \times PA \times (Y_{base} + \Delta Y) \quad [S2]$$

We next broke down equation [S2] into three components as,

$$P = (1 - \overline{f_{ab}}) \times PA \times Y_{base} + (\overline{f_{ab}} - f_{ab}) \times PA \times (Y_{base} + \Delta Y) + (1 - \overline{f_{ab}}) \times PA \times \Delta Y \quad [S3]$$

where $1 - \overline{f_{ab}}$ represents harvested area ratio in normal years; and $\overline{f_{ab}} - f_{ab}$ defines changes in abandonment for years of interest relative to the expected abandonment in normal years. We then extracted each of three components from [S3]:

$$P_{base} = (1 - \overline{f_{ab}}) \times PA \times Y_{base} \quad [S4]$$

$$\Delta P_{fab} = (\overline{f_{ab}} - f_{ab}) \times PA \times (Y_{base} + \Delta Y) \quad [S5]$$

$$\Delta P_Y = (1 - \overline{f_{ab}}) \times PA \times \Delta Y \quad [S6]$$

The f_{ab} and ΔY were simulated for the years of interest in our RF models (Eqs. [1] and [2] in Main text). Note that the average abandonment ($\overline{f_{ab}}$) and expected base yields (Y_{base}) in normal years were defined as the 30-year averages, calculated by using climate data from the period 1981-2010. We defined PA as the 30-year average over 1981-2010 when we calculated production changes due to abandonment and yield reductions. This allowed us to compare production losses from climate-driven changes in both abandonment and yields among years. The base abandonment ($\overline{f_{ab}}$) was calculated as,

$$\overline{f_{ab}} = \frac{1}{30} \sum_{y=1981}^{2010} fab_y \quad [S7]$$

The expected base yield (Y_{base}) was calculated from ΔY and average expected yield ($\tilde{Y}$) (e.g., 30-yr expectation value) derived from the loess regression,

$$Y_{base} = \frac{1}{30} \sum_{y=1981}^{2010} (\Delta Y_y + \tilde{Y}) \quad [S8]$$

We then examined and integrated county-level production for each component to state-

level production,

$$\Delta P_{fab,y} = \sum_{c=1}^n \Delta P_{fab,c,y} \quad [S9]$$

$$\Delta P_{Y,y} = \sum_{c=1}^n \Delta P_{Y,c,y} \quad [S10]$$

$$\widehat{P_{base}} = \sum_{c=1}^n P_{base,c} \quad [S11]$$

where y refers to specific year of interest (e.g., 2023), c represents specific county, n equals to 105 (number of counties in Kansas, U.S.). Lastly, we expressed production changes relative to climate-driven averaged production over 1981-2010 ($\widehat{P_{base}}$) as,

$$\%P'_y = \frac{\Delta P_{fab,y} + \Delta P_{Y,y}}{\widehat{P_{base}}} \times 100 \quad [S12]$$

where $\%P'$ is the relative production change (%) (shown in Figure 2.2 in Main text).

Text A.2. The most critical climate driver of abandonment or yield loss

While RF models have built-in methods for assessing the relative importance of predictor variables, such as feature importance, these methods typically assess variable importance at a global scale. No insight is given as to what is driving the prediction for a given observation point. Thus, in this study, we integrated a game theory (Shapley additive explanations, SHAP) into the RF models we created (equations [1] and [2] in Main text) to quantify the most critical climate drivers in wheat abandonment and yield changes. The SHAP values provide local model explanations and the contribution of each predictor variable for each data point via estimating the expected marginal contribution of a predictor across all possible combinations of predictors. Specifically, the magnitude of the SHAP value represents the strength of contribution to the

prediction. A larger absolute magnitude implies a stronger influence, while a smaller absolute magnitude indicates a weaker influence. We based our selection of predictors on the magnitudes for both directions (positive and negative). The more positive and more negative ones were selected as predictors. Moreover, a positive SHAP value means that it contributes to the increase in predicted value, and vice versa. Thus, we focused on the climate variables with more positive SHAP values for fab and with more negative SHAP values for ΔY .

The process to identify the climate drivers for yield and abandonment extremes includes five steps (Figure A.6): 1) we defined an extreme abandonment event as the abandonment above the 90th percentile, and an extreme yield losses event as the yield variation below the 10th percentile across all years (1926-2023) for each county in Kansas; 2) for each observed crop yield extreme event, we used SHAP to break down the predicted value derived from the RF model into the contribution of individual climate variables; 3) climate variables with the top three highest SHAP values and the top three lowest negative SHAP values were identified as the primary influencers for the abandonment and yield loss events, respectively; 4) based on the climate variables we used and the prevalent climate causes, we focused on four climate extreme events (low precipitation, high precipitation, cold temperatures, and warm temperatures) during four specific growth periods based on 10th or 90th percentiles of historical probability distributions. Note, a cold event occurs when T_n falls below its 10th percentile, whereas a warm event occurs when T_x exceeds its 90th percentile; 5) we determined the most critical climate driver for each abandonment or yield loss extreme. For example, for extreme abandonment, if the climate variable with the highest SHAP value (step 3) corresponded to any of four types of climate extremes above (step 4), it was deemed as the most pivotal climate extreme event; if no correspondence was found, we proceeded to look for the second highest variable, and subsequently to the third if necessary.

Finally, all extremes in abandonment (or yield) associated with the identical primary climate drivers were grouped together, resulting in 16 distinct groups. These groups were then used to calculate the percentage of area driven by the same primary driver relative to the total area experiencing extreme abandonment (or yield losses).

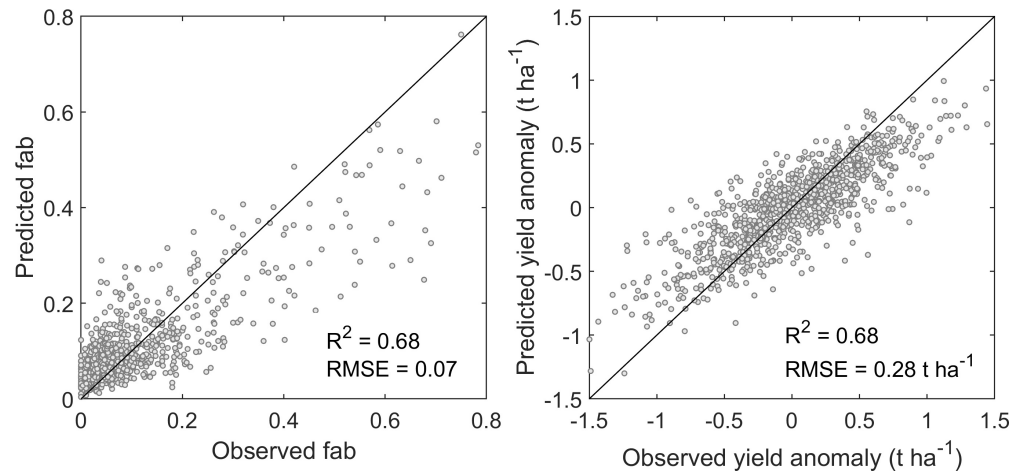


Figure A.1. Predicted vs. observed abandonment rates (fab) and yield anomaly (t ha^{-1}). Black lines represent the 1:1 line. We showed the coefficient of determination (R^2) and root mean square error (RMSE).

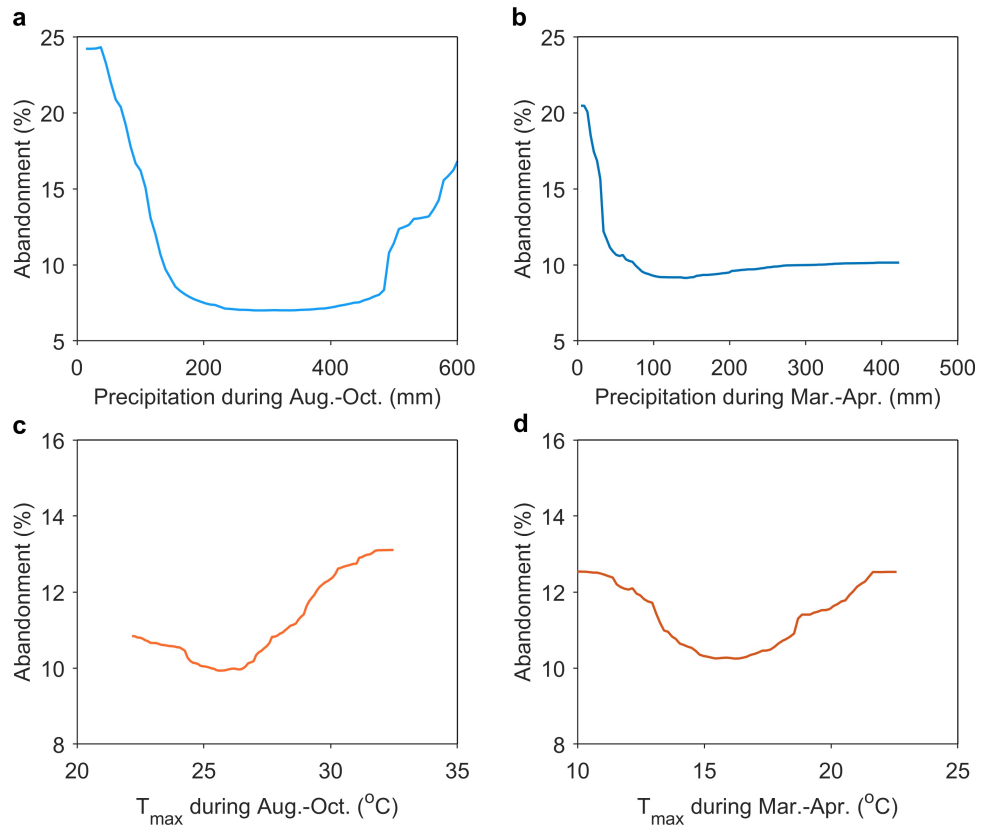


Figure A.2. Partial response of crop abandonment to precipitation in Fall (a) and Spring (b), as well as to maximum temperature in Fall (c) and Spring (d) taken from our random forest (RF) model.

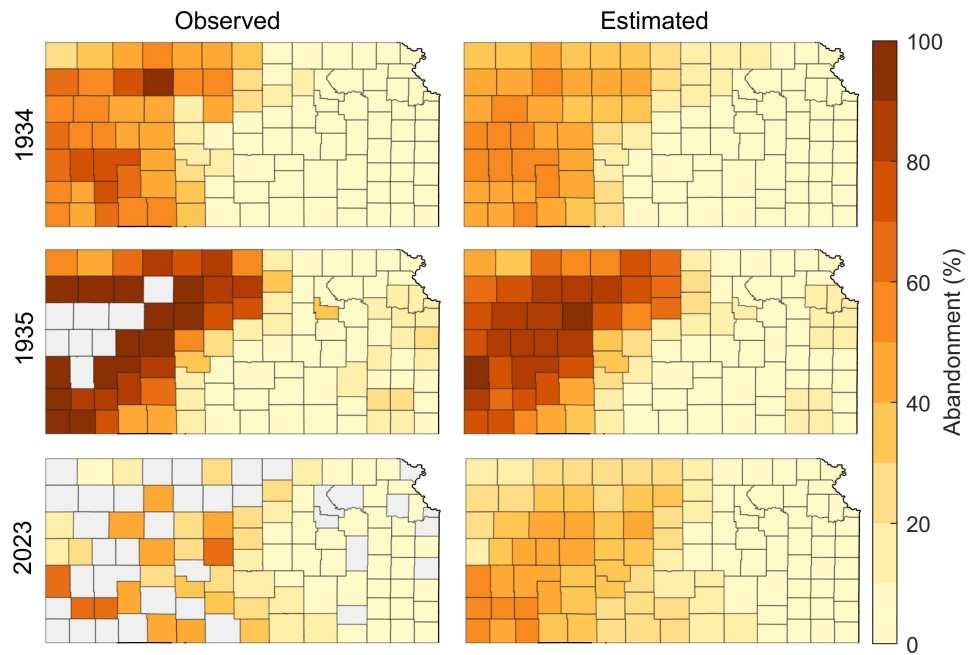


Figure A.3. Robustness check of the estimation. Spatial distributions of the observed and estimated abandonment in typical years (1934, 1935, and 2023). The gray regions for the observed abandonment in 1935 and 2023 panels represent areas where county-level data on areas were unavailable.

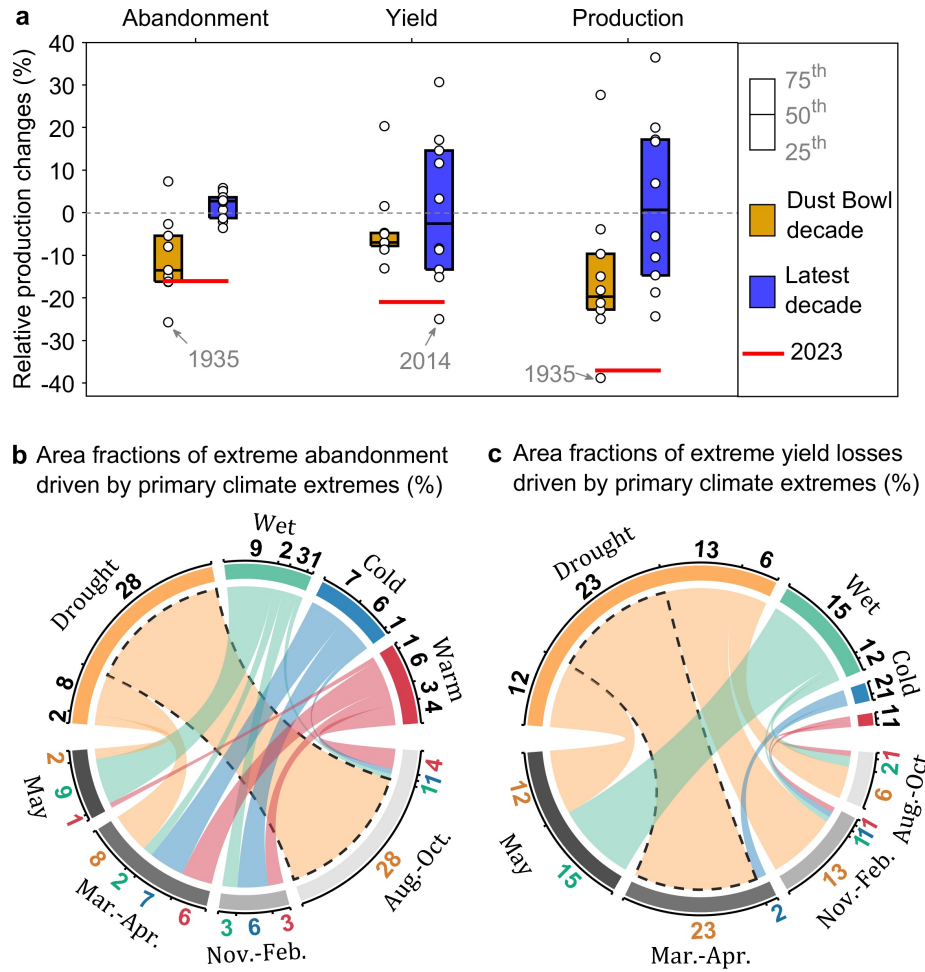


Figure A.4. The decomposition of wheat production and primary climate drivers of extreme abandonment and yield loss. Similar to Figure 2.2b and Figure 2.3e,f, but the accumulated precipitation was replaced with the Palmer Z Index in the models.

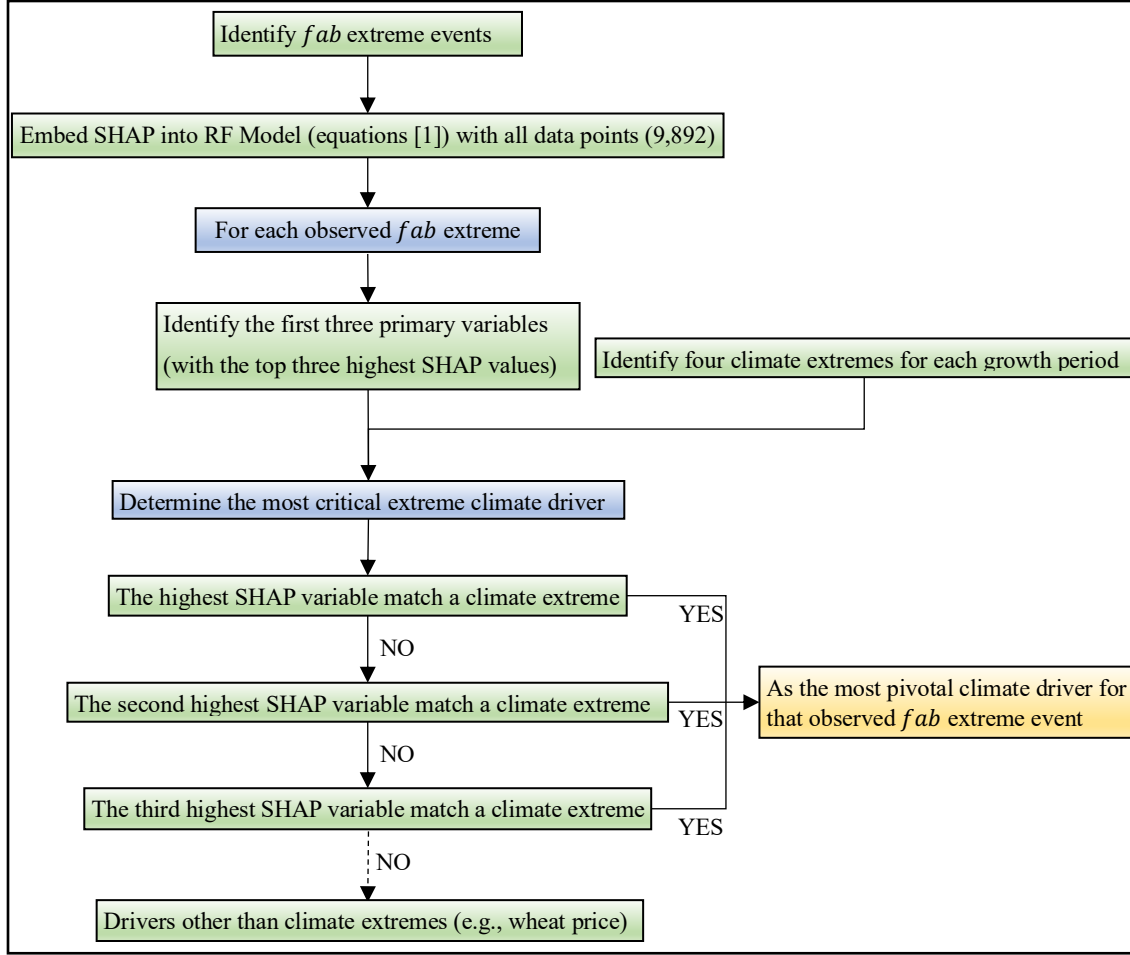


Figure A.6. Workflow of identifying the critical climate driver of each extreme abandonment. This workflow was also carried out for the extreme yield loss (ΔY ; equation [2] in the main text), but using the lowest SHAP variable. This process was repeated for each observed extreme abandonment or yield loss occurrence. After the workflow, all extremes in abandonment or yield losses associated with the same primary climate driver were used to calculate the area fraction. Additionally, the area fraction for extremely low wheat prices (<10th) for *fab* was also calculated. The detailed descriptions can be found in Supplementary Text A.

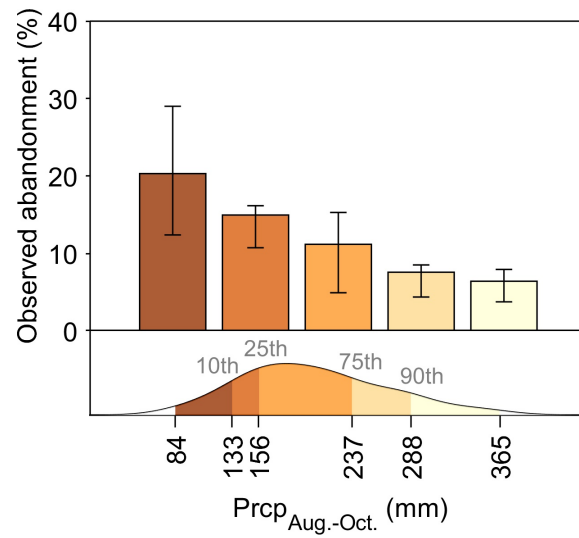


Figure A.7. Effects of fall precipitation on wheat abandonment in Kansas. The state-level observed abandonment (%) binned over fall precipitation (Prdp) from 1926-2023. The error bars indicate the 25th and 75th percentiles across all years within each precipitation bin. The lower panel displays the state-level precipitation distribution color-coded over 1926-2023 and precipitation percentiles are shown for defining the bins used.

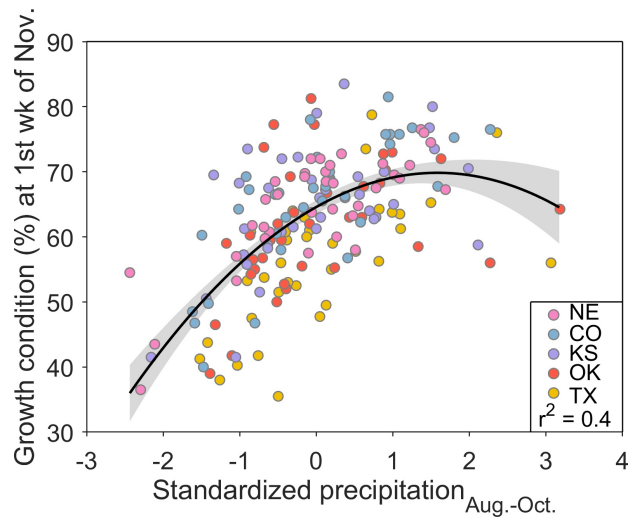


Figure A.8. Relationship between wheat growth index conditions and precipitation in early November (first week) from 1987 to 2023. The quadratic relationship between winter wheat growth conditions and precipitation during August-October across the five wheat states (Nebraska, NE; Colorado, CO; Kansas, KS; Oklahoma, OK; and Texas, TX). State-level growth conditions were derived from USDA-NASS.

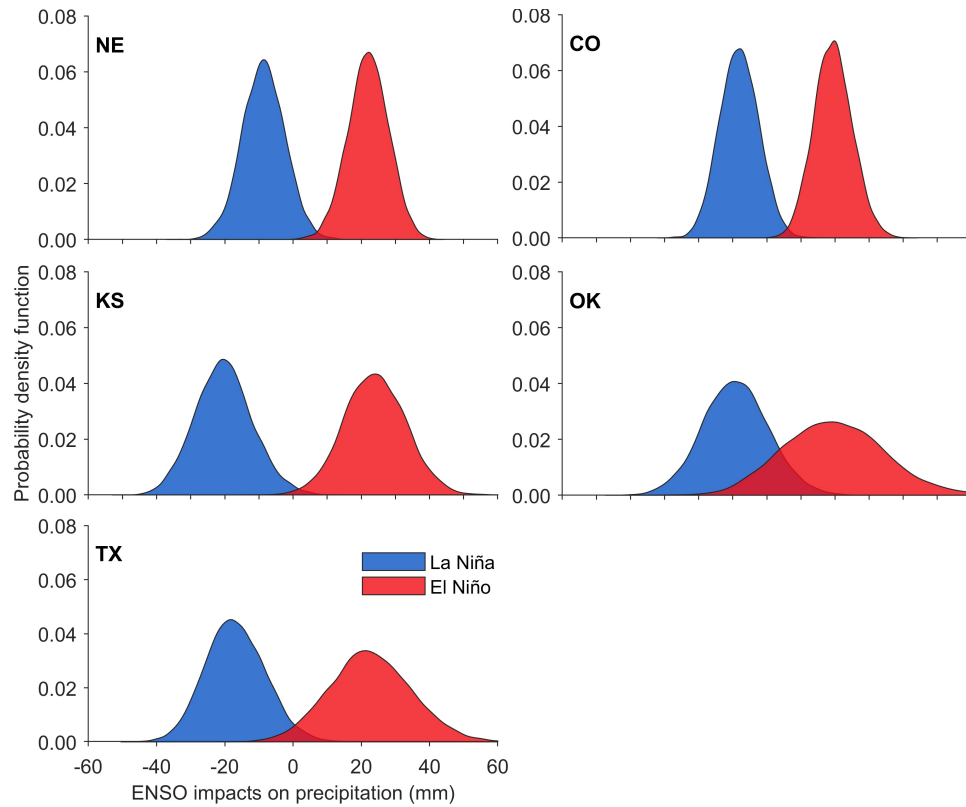


Figure A.9. Impacts of ENSO phases on linear detrended precipitation anomalies. Distributions of area-weighted average fall precipitation anomalies during El Niño (red) and La Niña (blue) phases in Nebraska (NE), Colorado (CO), Kansas (KS), Oklahoma (OK), and Texas (TX) based on average harvested area during 1981-2010. Negative and positive values indicate ENSO phases with decreased and increased precipitation, respectively. Distribution of precipitation anomalies in both El Niño and La Niña phases were plotted based on bootstrapping approach ($n = 10,000$) (see Main Methods).

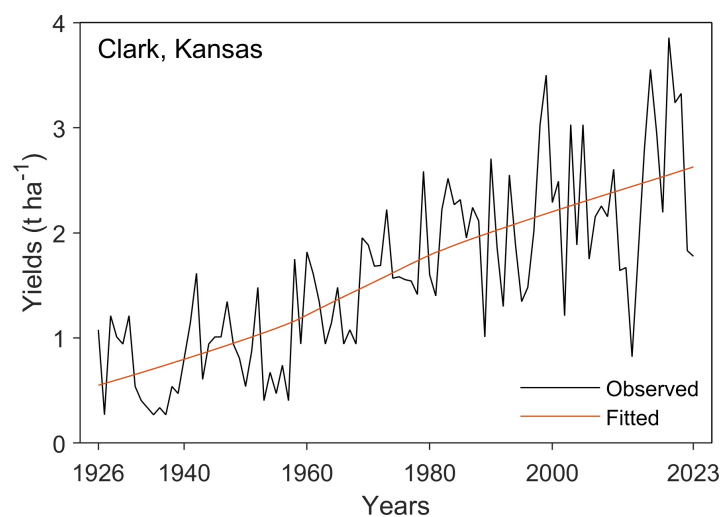


Figure A.10. An example of yield trend used in this study through locally weighted smoothing regression with a span parameter of 0.75.

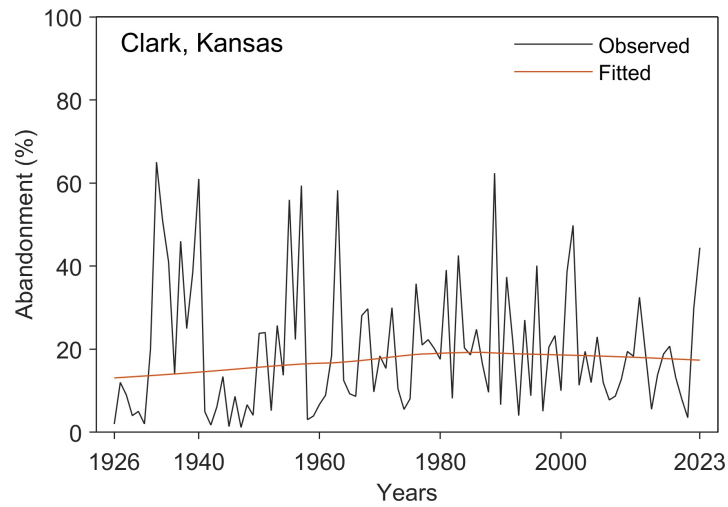


Figure A.11. An example of crop abandonment variations (Clark County in Kansas) with a locally weighted smoothing regression (a span of 0.75) used for detrending process.

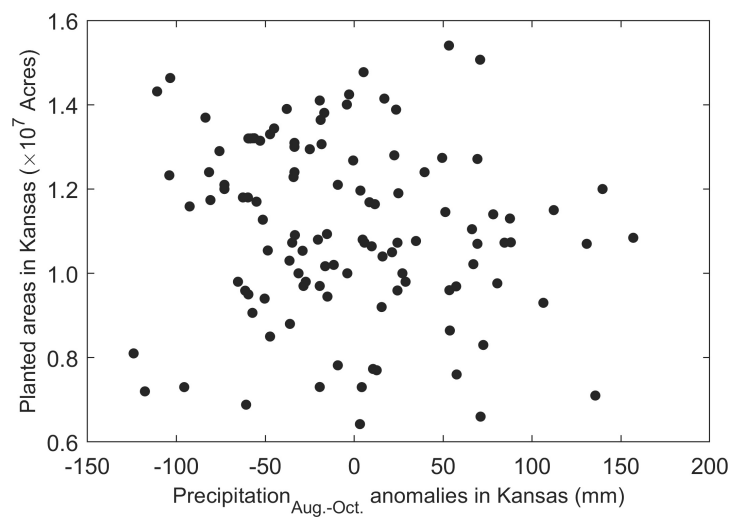


Figure A.12. State-level planted areas of winter wheat vs. pre-season precipitation anomalies (with a base period of 1981-2010) across 1909-2023 in Kansas. Planted area data were derived from the United States Department of Agriculture-National Agricultural Statistics Service (USDA-NASS).

Table A.1. Modeling performance.

Models	Yield changes		Abandonment fraction	
	R ²	RMSE (t ha ⁻¹)	R ²	RMSE (-)
Model 1 (Prcp, Tx, and Tn)	0.68	0.28	0.68	0.07
Model 2 (Palmer Z-Index, Tx, and Tn)	0.70	0.27	0.65	0.08
Model 3 (Prcp, f _{wd} , and f _{cd})	0.70	0.27	0.69	0.07

Notes: Model 1 is the model we used in Main text with predictors including the accumulated precipitation (Prcp), mean maximum temperature (Tx), and mean minimum temperature (Tn) during four specific growth periods (fall, winter, spring, and early summer). In Model 2, the Prcp was replaced with the Palmer Z-Index. We also substituted the Tx and Tn in Model 1 by the fraction of warm days (f_{wd}) and cold days (f_{cd}) for Model 3.

Table A.2. Available years for planted and harvested areas data from USDA-NASS.

States	County-level	State-level
Nebraska	1956 - 2023	1909 - 2023
Colorado	1929 - 2023	1909 - 2023
Kansas	1926 - 2023	1909 - 2023
Oklahoma	1926 - 2023	1909 - 2023
Texas	1968 - 2023	1909 - 2023

Appendix B - Supplemental Information for Chapter 3

Text B.1. Phenology of winter wheat

We collected phenological observations including planting dates for 119 locations and harvest dates for 101 locations (excluding Texas (TX)) from the dryland field trials (Table B.1). Note, even though harvest dates in TX are not available, we collected the observed heading dates from the Agricultural Research Service covering three locations (Figure B.3 and Table B.1). We used a previous approach¹ to fill in planting and harvest dates for missing years in each location from 1982-2020.

The growing degree days (GDD, °C days) is a common matrix used to partition phenological periods of crops^{2,3}. To gain the heading and jointing dates, we first calculated the state-level heading and harvest dates following the previous approach⁴ based on the weekly state-level progress report from the United States Department of Agriculture's National Agricultural Statistical Service's (USDA-NASS) from 1982-2020. We then combined the state-level phenology with local temperatures³ to obtain the site-level GDD ratio from January 1 to heading dates and to maturity dates (referred to as RHM_{site} ranging from 55% to 60%). The maturity dates were inferred from dates 14 days prior to harvest dates⁵. Next, the site-level GDD ratio from January 1 to the jointing date and to maturity date (referred to as RJM_{site}) was estimated using the RHM_{site} based on a fixed ratio ($RJM_{site} : RHM_{site} = 35\% : 57\%$)^{1,2}. Finally, the jointing and heading dates were estimated for each site-year using the RJM_{site} and RHM_{site} . Note that the observed heading dates in TX were collected over 20 years covering three stations including Bushland, Chillicothe, and Dallas, which represent three diverse natural regions: Great Plains, North Central Plains, and Coastal Plains, respectively (red dots in Figure B.3c and Table B.1). Thus, we estimated maturity dates in TX based on the accumulated GDD from January 1 to heading date and RHM_{site} . Then,

similar to other sites, the phenological dates for sites within TX were also estimated. Finally, the life cycle of winter wheat was segmented into three phenological periods: planting to jointing (p1), jointing to heading (p2), and heading to maturity (p3) for each location-year (Figure B.3).

Text B.2. Climate covariates

We first calculated two climate covariates including GDD and a linear and squared cumulative precipitation (Prcp, mm) for three phenological periods. The GDD was calculated based on adjusted mean temperature³ by imposing a maximum of 30°C and a minimum of 0°C⁶ on the daily minimum and maximum temperatures. The cold stress and heat stress were then tracked through the freeze degree days (FDD, °C days) and extreme degree days (EDD, °C days), respectively, quantified as:

$$FDD = \sum_{h=1}^H DD_h \quad DD_h = \begin{cases} 0 & \text{if } T_h \geq T_{low} \\ \frac{|T_h - T_{low}|}{24} & \text{if } T_h < T_{low} \end{cases} \quad (S1)$$

$$EDD = \sum_{h=1}^H DD_h \quad DD_h = \begin{cases} 0 & \text{if } T_h < T_{high} \\ \frac{(T_h - T_{high})}{24} & \text{if } T_h \geq T_{high} \end{cases} \quad (S2)$$

The hourly temperatures (T_h) were simulated from daily maximum and minimum temperatures⁷. DD_h represents degree days for hour h , and H is the number of hours in the specific phenological period. The T_{low} (-11°C and -1°C during p1 and p2 periods, respectively)⁸ and T_{high} (30°C during p2 and p3 periods)⁶ are common stress thresholds for the development in winter wheat.

Text B.3. Identification of cultivar groups

We identified 58 cultivar subsets (or groups), each comprising cultivars released over at least 10 distinct release years and tested across at least 10 environments (or site-years), based on a

structured six-step selection procedure (Figure B.4):

(1) Site-year filtering: We began with 1,726 total site-years and excluded those containing cultivars from fewer than 10 unique release years, retaining 585 qualified site-years for further analysis.

(2) Defining cultivar co-occurrence groups based on reference site-years: For each of the 585 qualified site-years, we treated the set of cultivars tested in that site-year as a seed group. We then scanned all other site-years to identify environments in which any of those same cultivars co-occurred. This allowed us to construct a cultivar group tested under the same environments. For each group, we built a matrix with rows representing the cultivars from the reference site-year and columns representing all site-years in which at least one of those cultivars was also grown. The yield of each cultivar in each site-year was recorded when available, and missing values (where a cultivar was not grown in a given site-year) were assigned as ‘Not a Number; NaN.’ This procedure generated 585 initial groups, each capturing cultivar performance across the environments where seed group cultivars co-occurred.

(3) Within-group filtering: For each of the 585 groups, we excluded cultivars (rows) appearing in less than 10 site-years and removed site-years (columns) with less than 10 unique cultivar release years or with more than two missing data points. This step ensured that each group retained cultivars and environments with sufficient representation for reliable trend estimation.

(4) Removal of small groups: After filtering, we further removed any groups that contained fewer than 10 site-years or fewer than 10 unique cultivar release years. This final filtering step ensured that only groups with adequate environmental and temporal breadth were retained. As a result, 257 groups were available for the next phase of analysis.

(5) Removal of redundant groups: Across the 257 retained groups, we identified redundant groups, defined as those sharing more than 90% of the same site-year-cultivar observations. For each set

of near-duplicate groups, we only utilized the group with the largest number of cultivars to preserve the most informative instance. This filtering step reduced the number of groups to 70, with an average pairwise overlap of only 20% (site-year-cultivar observations), indicating broad independence among the groups.

(6) Filtering based on environmental range: Finally, to ensure a sufficient range of stress conditions, we retained groups with an environmental index (EI) range of at least 3 t ha⁻¹, where EI was used to quantify environmental stress level and calculated based on the average yield of all cultivars per site-year within each group. This last step yielded 58 groups used to analyze how breeding-driven yield gains vary across different environmental stress levels.

Text B.4. Benchmark-based assessment of cultivar yield trends

We selected a long-term wheat cultivar ‘Arapahoe’ (released in 1988) to use as a reference. It had the longest trial period among all cultivars studied and was widely planted in 438 site-years. To ensure reliable comparison of cultivar performance across diverse environments, we implemented the following mathematical coding flow:

(1) Define yield environment using Arapahoe’s yield percentiles (Figure B.6a)

Define:

$Y_{\text{ref},25}$ = 25th percentile of Arapahoe’s yield across all 438 site-years (i.e., 2.6 t ha⁻¹),

$Y_{\text{ref},75}$ = 75th percentile of Arapahoe’s yield across all 438 site-years (i.e., 4.2 t ha⁻¹),

For each site-year (e), compare Arapahoe’s yield:

If $Y_{\text{ref},e} \leq Y_{\text{ref},25}$, classify as a low-yielding environment

If $Y_{\text{ref},e} \geq Y_{\text{ref},75}$, classify as a high-yielding environment

Otherwise, classify as a moderate-yielding environment (not adjusted)

(2) Calculate adjusted yield for each cultivar (normalization) (Figure B.6b-f)

Define:

$Y_{c,e}$: observed yield of cultivar c in the site-year e

$Y_{ref,e}$: Arapahoe's observed yield in the site-year e

$\overline{Y_{ref,LY}}$: Arapahoe's average yield under low-yielding (LY) environments (i.e., 2.0 t ha⁻¹)

$\overline{Y_{ref,HY}}$: Arapahoe's average yield under high-yielding (HY) environments (i.e., 4.8 t ha⁻¹)

$Y_{c,e}^{adj}$: adjusted yield of cultivar c in the site-year e

Then:

For low-yielding site-years,

$$Y_{c,e}^{adj} = Y_{c,e} + (\overline{Y_{ref,LY}} - Y_{ref,e})$$

For high-yielding site-years,

$$Y_{c,e}^{adj} = Y_{c,e} + (\overline{Y_{ref,HY}} - Y_{ref,e})$$

For moderate-yielding site-years,

$$Y_{c,e}^{adj} = Y_{c,e} \quad (no\ adjustment)$$

(3) Estimate breeding-driven yield trend for low- and high-yielding environments

To ensure a consistent basis for comparison, we retained only those cultivars that simultaneously appeared in both low- and high-yielding environments. Specifically, we first identified cultivar release years under each environmental type (Figure B.6g), and then determined the subset of cultivars shared between both environmental types within the same release year (Figure B.6h). For example, of all five cultivars released in 2010, 'McGill' and 'Robidoux' were the only two observed in both low- and high-yielding site-years, making them eligible for comparison. Lastly, yield trends over cultivar release years were estimated separately for low- and high-yielding environments (Figure B.6i).

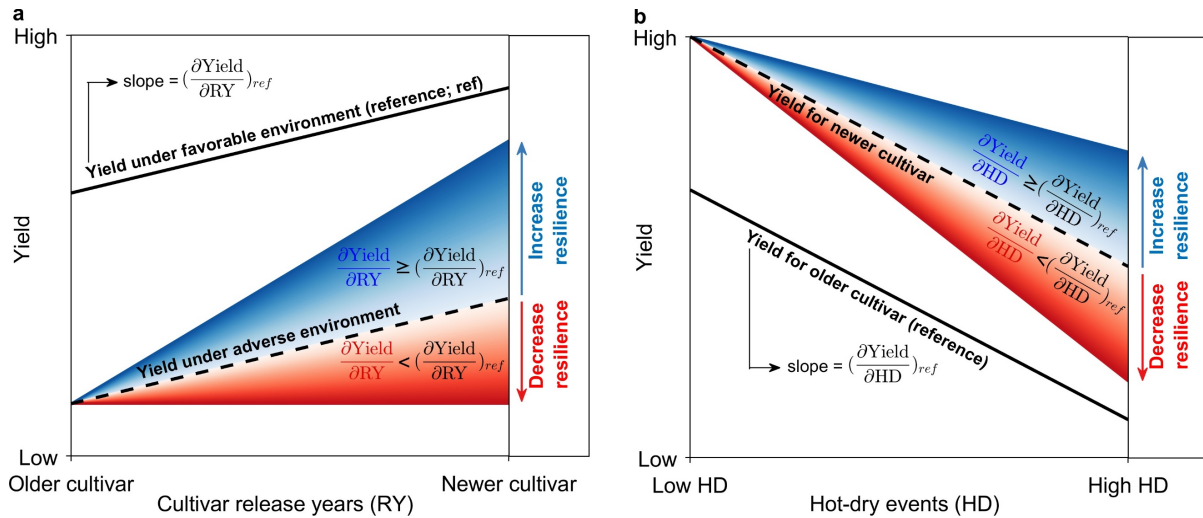


Figure B.1. Conceptual diagram illustrating scenarios of breeding-driven climate resilience. a, Breeding-driven yield trends under favorable and adverse environments. The solid black line shows yield improvements under favorable environments, serving as a reference here for evaluating changes in climate resilience. The dashed black line, parallel to the solid black line, indicates consistent yield improvements under adverse environments. Blue shading (including dashed line) denotes increased resilience where cultivar advancements sustain consistent or greater yield gains under adverse conditions. Red shading indicates declining resilience, where yield gains are slower under adverse conditions than under favorable conditions. b, Yield change of newer vs. older cultivars under hot-dry (HD) stress conditions. The solid black line represents the yield change between low and high HD stress for older cultivars, and it serves as a reference for assessing changes in HD resilience. The dashed black line, parallel to the solid black line, indicates consistent yield loss for newer cultivars. Blue shading (including dashed line) reflects increased HD resilience, where newer cultivars exhibit consistent and even smaller yield losses under HD stress compared to older ones. Red shading indicates declining HD resilience where newer cultivars suffer more negative yield losses than older ones.

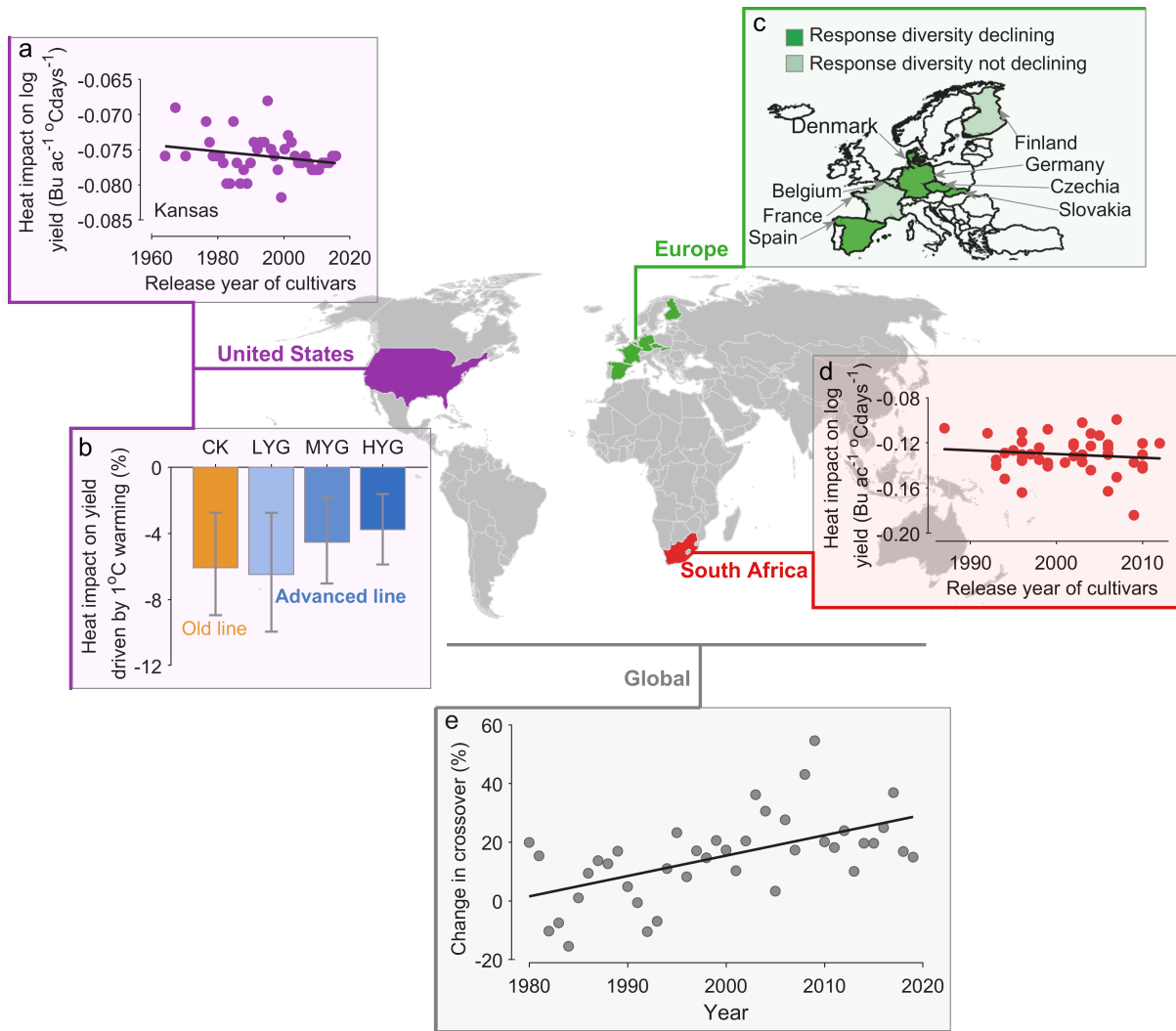


Figure B.2. Change in response of wheat breeding progress to climate resilience from current existing studies, including in Kansas, U.S. (a)⁹, U.S. Great Plains (b)¹⁰, Europe (c)¹¹, South Africa (d)¹², and International Wheat Improvement Network's Elite Spring Wheat Yield Trial (e)¹³. Data sources used in all sub-figures were taken from references cited here.

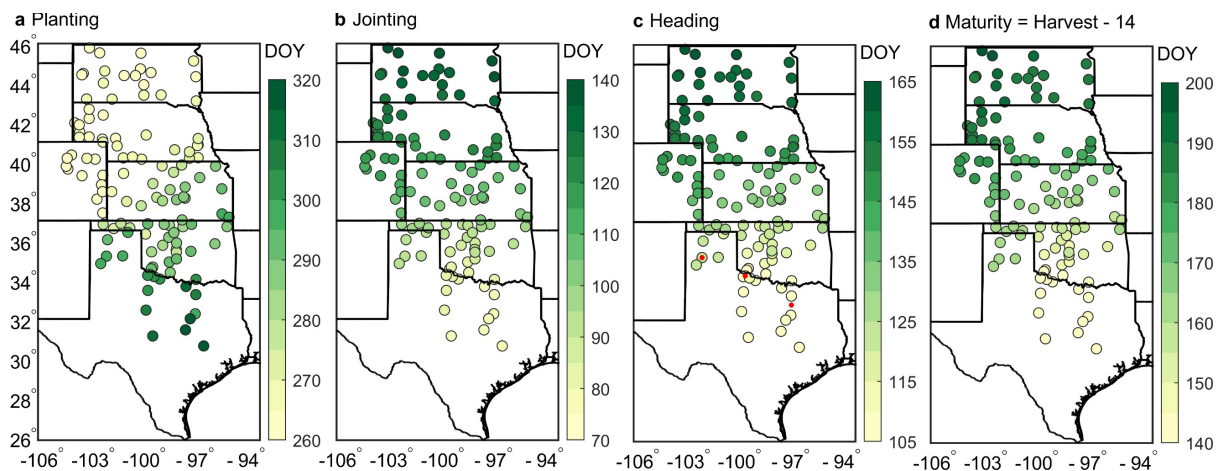


Figure B.3. Average phenology (days of year, DOY) estimated from 1982 to 2020. a-d, The estimated phenology included planting (a), jointing (b), heading (c), and maturity (d) dates. The three red dots in Texas in c denote three stations where the heading dates were documented by observations.

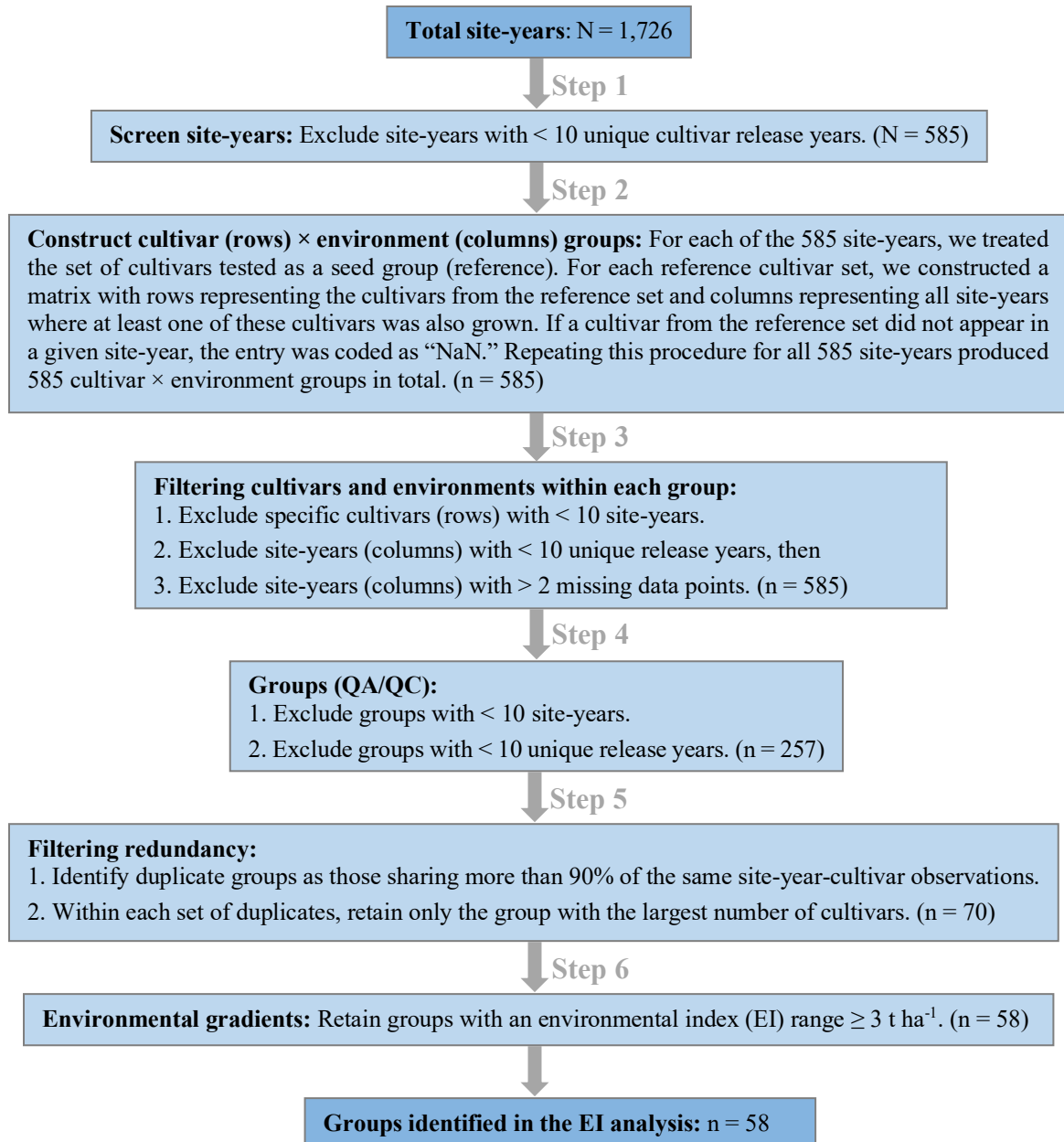


Figure B.4. Flowchart for identifying cultivar × environment groups used in the environmental index (EI) analysis. ‘N’ denotes the number of site-years, and ‘n’ represents the number of cultivar × environment groups retained at each step.

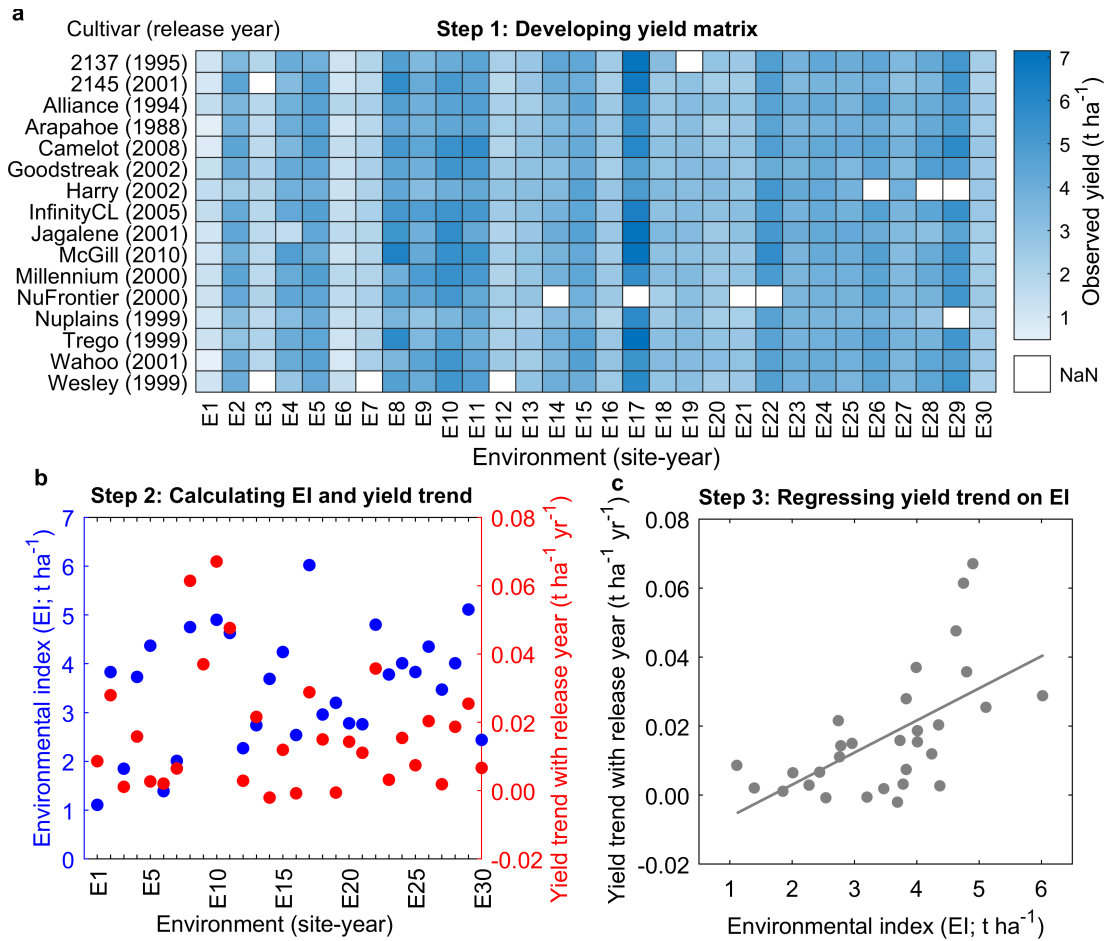


Figure B.5. Diagram illustrating the change of breeding-driven yield gains over the environmental index (EI). a, A 16×30 yield matrix for a selected group, with rows representing cultivars and columns representing environments (site-years). ‘NaN’ refers to missing data. We ensured that missing data did not exceed two entries for each site-year to avoid overly unbalanced data. b, EI (blue dots) and breeding-driven yield trend (red dots) calculated for each site-year within the group. c, The relationship between breeding-driven yield trends and EI across all environments where the solid line represents a linear regression fit.

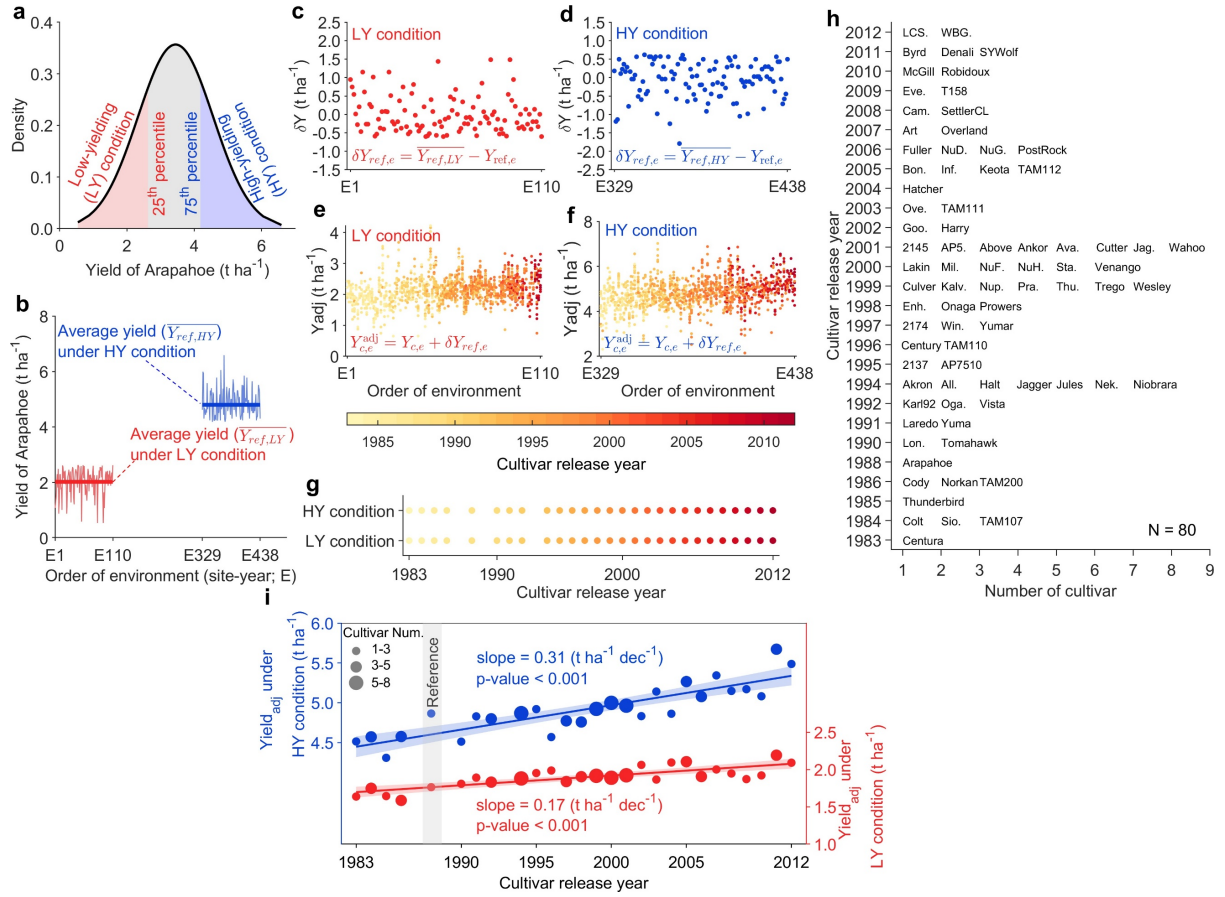


Figure B.6. Detailed procedures of breeding-driven yield trends under low- (LY) and high-yielding (HY) environments, using a reference cultivar ‘Arapahoe.’ a, Yield distribution of ‘Arapahoe’ across 438 site-years. LY (red shading) and HY (blue shading) environments were defined based on the 25th and 75th percentiles, respectively. b, Arapahoe’s yields in LY (red lines) and HY (blue lines) environments. The horizontal line denotes Arapahoe’s average yield ($\bar{Y}_{ref}$). c,d, Arapahoe’s yield deviation (δY) between its average yield under LY (c) or HY (d) environments and its observed yield. e,f, Adjusted yields (Y_{adj}) of cultivars in LY (e) and HY (f) environments, normalized to Arapahoe’s average yield in LY and HY environments, respectively, for all site-years identified. g, Cultivar release years identified in both LY and HY environments. h, Shared cultivars planted in both LY and HY environments for each release year. Some cultivar names were abbreviated due to space constraints. ‘N’ refers to the total number of cultivars. i, Changes in average adjusted yield across release years under LY (red dots) and HY (blue dots) environments. The size of the circle shows the number of cultivars shown in h. Solid lines and shaded areas are linear regression trends and the 95% confidence intervals, respectively. The gray shaded region marks the reference cultivar ‘Arapahoe.’

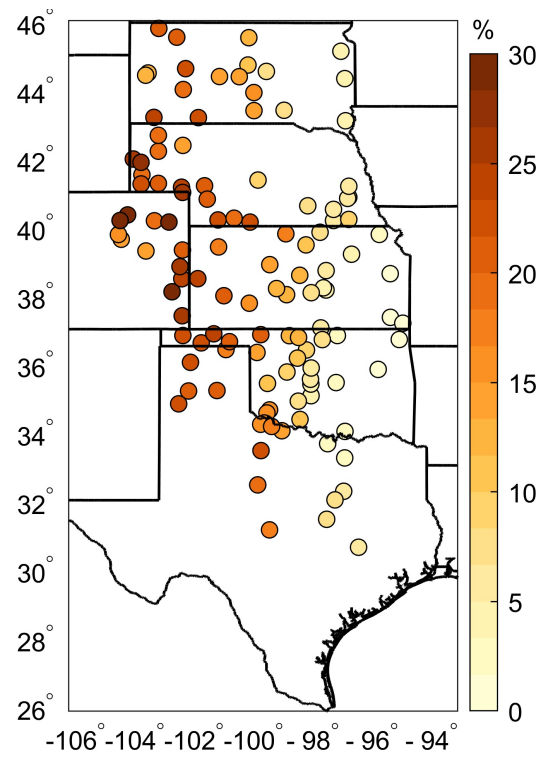


Figure B.7. Annual mean frequency of hot-dry events from heading to maturity period during 1982-2020.

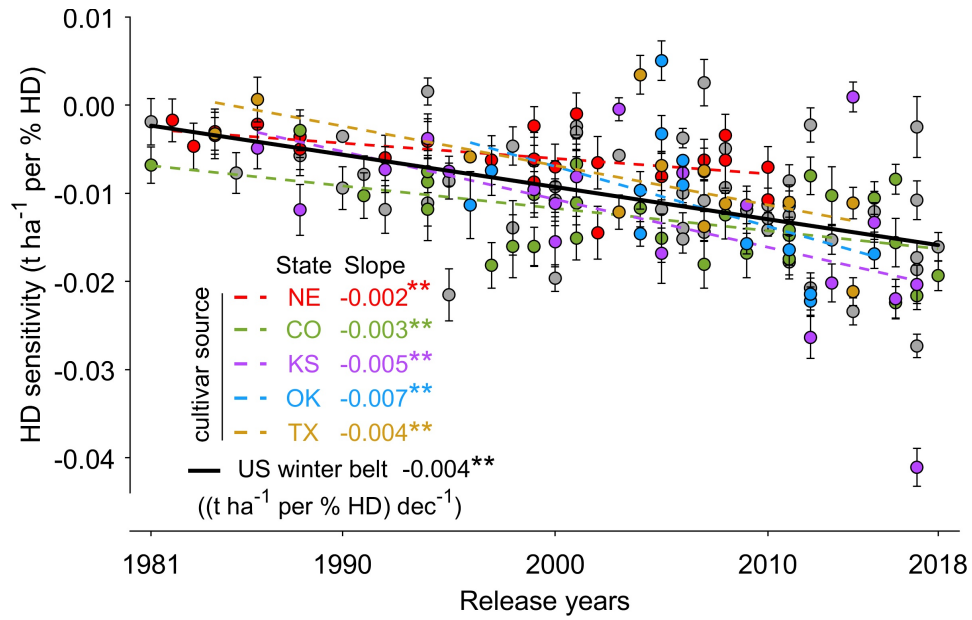


Figure B.8. Estimated sensitivity to hot-dry events (HD) across all cultivars. Cultivar release sources are color-coded: red for Nebraska (NE), green for Colorado (CO), purple for Kansas (KS), blue for Oklahoma (OK), yellow for Texas (TX), and gray for other sources like private companies. The state sources generally represent the corresponding State Universities. Error bars show mean $\pm$ one clustered SE. Dashed lines and solid black lines represent linear regression trends for specific cultivar sources (color-coded) and all data sources, respectively. The “**” denotes a statistical significance at the 95% confidence levels based on the Mann-Kendall test.

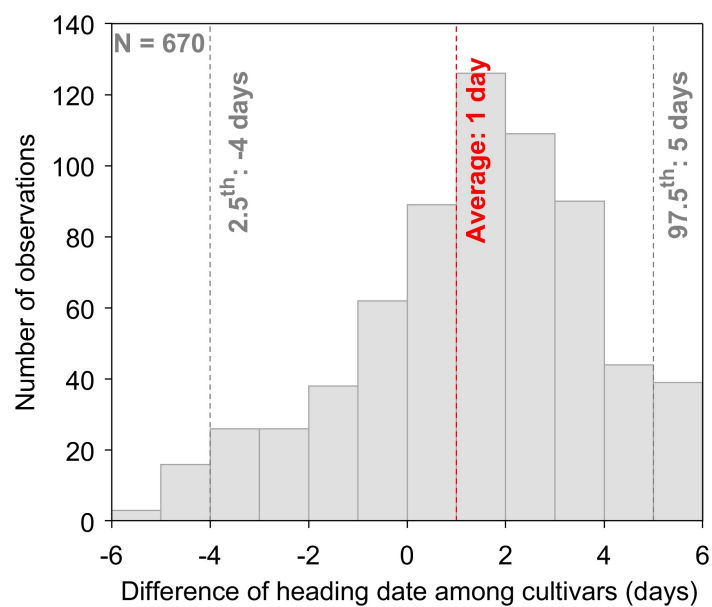


Figure B.9. Distribution of heading date difference among all cultivars evaluated at each site-year in Kansas from 1996 to 2013, along with three reference cultivars of 2137, Jagger, and Everest selected. The N = 670 is the available number of site-year-cultivar observations.

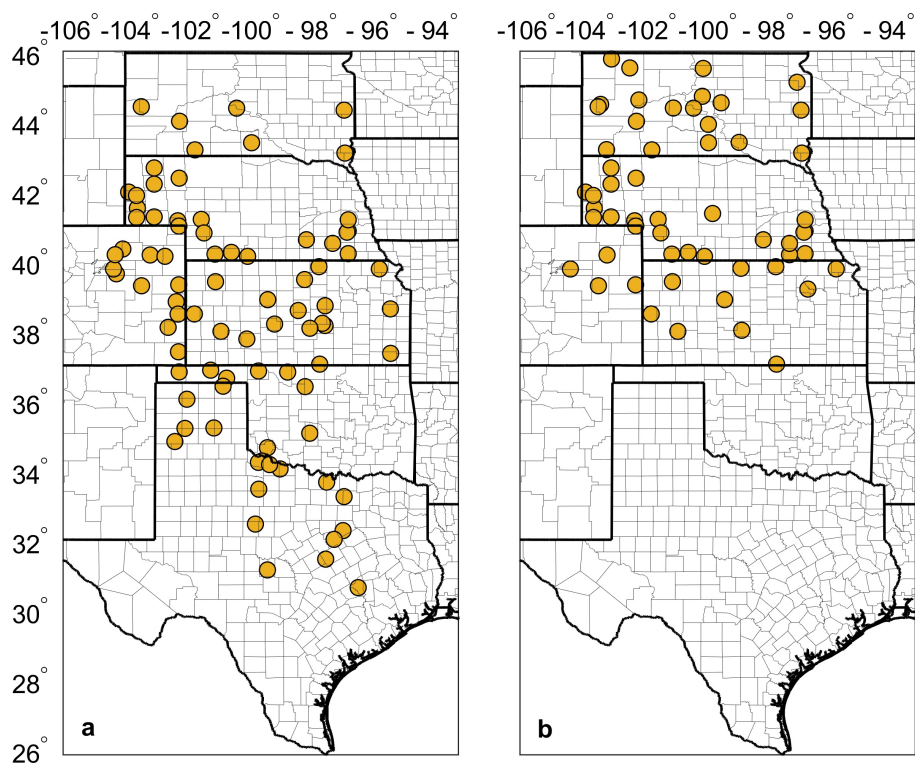


Figure B.10. Spatial distribution of trial sites selected for assessing the response of cultivar advancements to environmental stress. a, Distribution of 83 sites included for the environmental index analysis. b, Distribution of 56 sites included for the reference cultivar analysis.

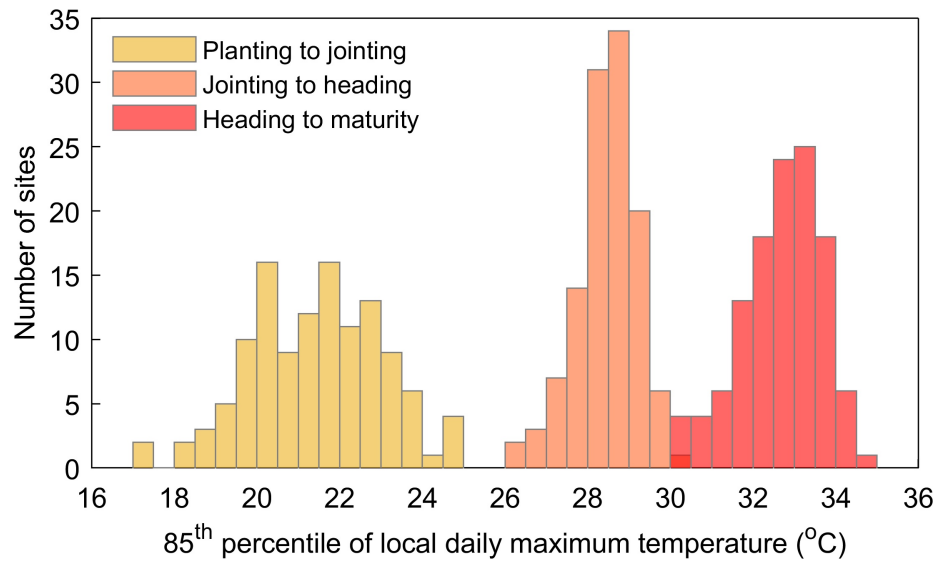


Figure B.11. Distribution of the local 85th percentile of daily maximum temperatures during specific phenological periods from 1982 to 2020.

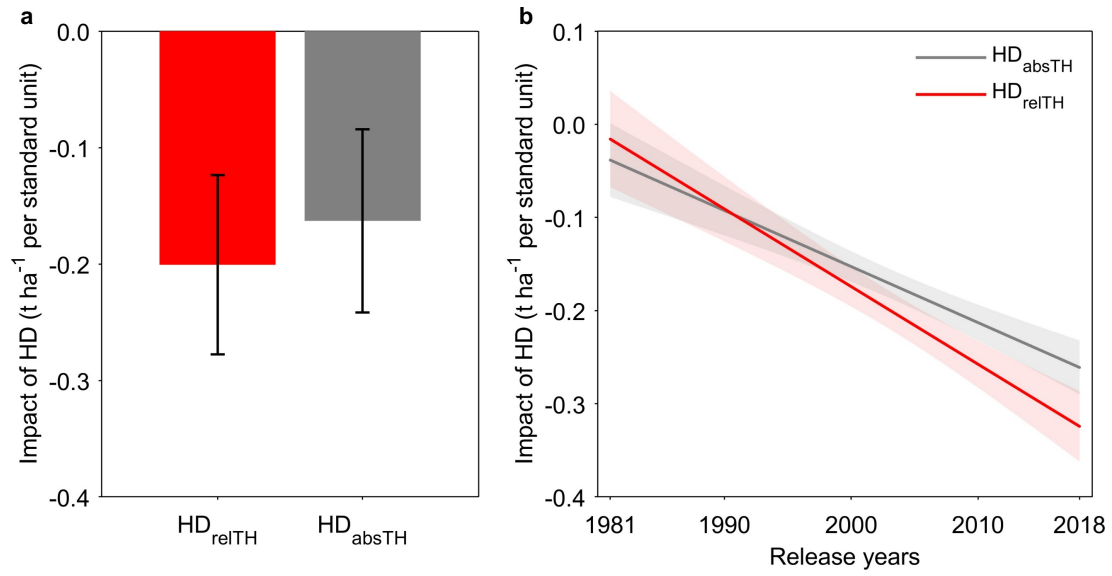


Figure B.12. The impact of hot-dry events (HD) on wheat yield, with HD estimated using absolute (HD_{absTH}) and relative thresholds (HD_{relTH}). a, Average yield loss associated with HD events, expressed per standard unit (or standard deviation) of HD events. Error bars represent the 95% confidence intervals. b, Changes in the sensitivity to HD across cultivar release years. The solid lines represent average impact, with shaded areas representing the 95% confidence intervals.

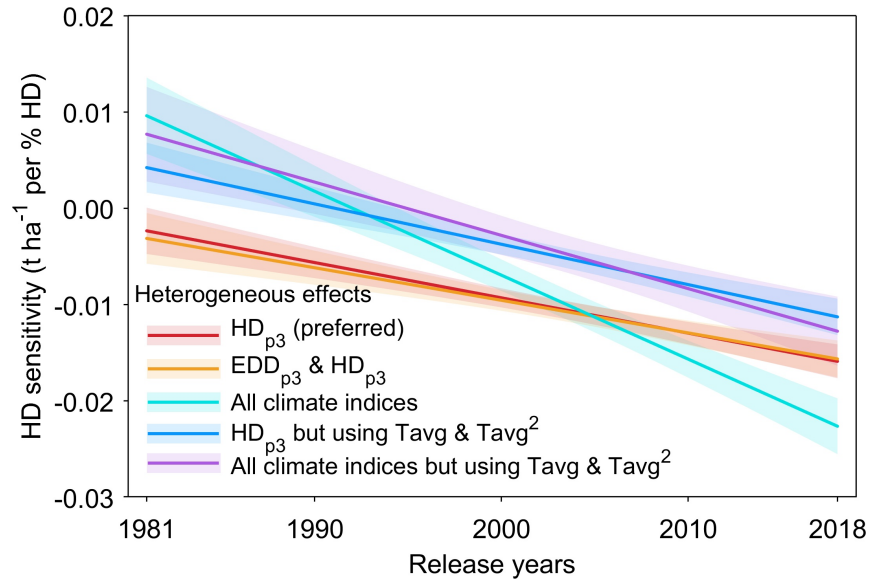


Figure B.13. Alternative models to estimate the change of sensitivity to hot-dry events (HD). The preferred model allows the effect of HD during heading to maturity period (p3) to vary across cultivars. The second model allows the effects of extreme degree days (EDD) and HD during the p3 period to vary, and the third model allows all climate indices to vary across cultivars. Additionally, we also replaced the temperature indices (growing degree days, GDD; freezing degree days, FDD; and EDD) during specific phenological periods with average temperature (Tavg) and a quadratic term (Tavg²) during three phenological periods to estimate the HD sensitivity by allowing HD or all climate variables to vary. The lines are linear regression fits estimated by the least squares, with shading representing the respective 95% confidence intervals.

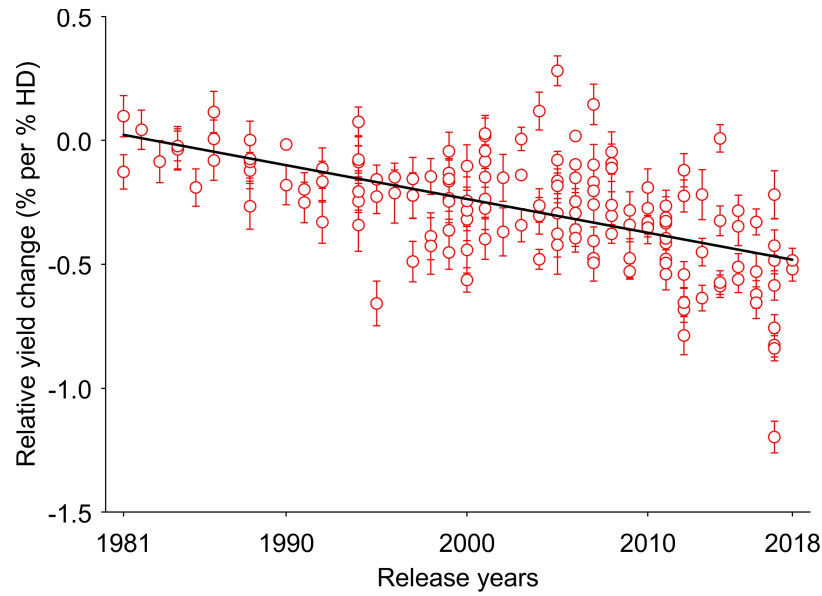


Figure B.14. Sensitivity of winter wheat cultivar advancement to hot-dry events (HD), estimated based on relative yield change (%). Estimated HD sensitivity across all cultivars, where each open circle represents a newly released cultivar in the U.S. hard winter wheat belt. Error bars show mean ± 1 SE. The solid black line represents the linear regression trend over cultivar release years.

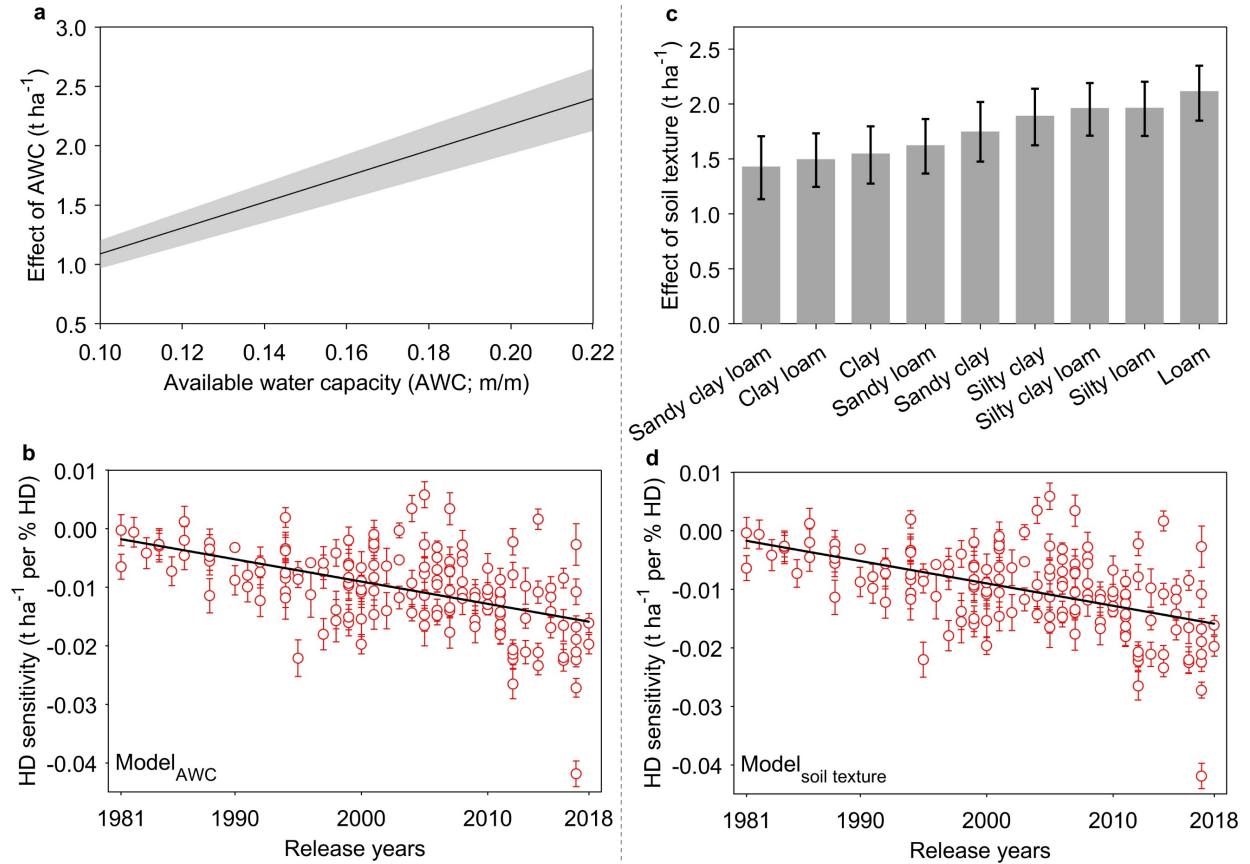


Figure B.15. Changes in sensitivity of wheat cultivars to hot-dry (HD) events based on models incorporating available water capacity (AWC) and site-level soil texture. a, The linear effect of AWC on yield. Black line shows the average effect, and the shaded area indicates the 95% confidence interval. The AWC data were extracted from the nearest 1-km ($\sim 0.009^\circ$) grid cell to each trial location based on the Gridded National Soil Survey Geographic Database (gNATSGO)¹⁴. b, Change in HD sensitivity over cultivar release years, accounting for AWC in the model ($Model_{AWC}$). c, Estimated effects of soil texture on yield. The soil texture for field-trial sites was obtained from the test reports used in this study. Bars refer to average effects with error bars showing the 95% confidence intervals from 500 bootstrap samples. d, Same as b but with soil texture included in the model ($Model_{soil\ texture}$).

Table B.1. Links to public datasets for crop and climate data.

Crop datasets	Links
South Dakota	https://extension.sdstate.edu/winter-wheat-variety-trial-results https://openprairie.sdstate.edu
Nebraska	https://digitalcommons.unl.edu/extensionhist/ https://cropwatch.unl.edu/winter-wheat-variety-test-results/
Colorado	https://csucrops.org/winter-wheat/ http://ramwheatdb.com/singlelocation.php
Kansas	https://www.ksre.k-state.edu/historicpublications/report-progress.html
Oklahoma	http://croptrials.okstate.edu/wheat/grain-yield https://digitalprairie.ok.gov/digital/collection/stgovpub/id/23998 https://www.okwheat.org/research-documents/variety-trials/ https://agresearch.okstate.edu/facilities/oklahoma-panhandle-research-and-extension-center/site-files/docs/wheat-performance-trials/2012-panhandle-osu-wvt.pdf
Texas	http://varietytesting.tamu.edu/wheat/ https://www.ars.usda.gov/plains-area/lincoln-ne/wheat-sorghum-and-forage-research/docs/hard-winter-wheat-regional-nursery-program/pre-2010-nursery-data/
Texas heading dates	
Cultivar release years	https://thewheatfarmer.com/wheat-varieties/
State-level progress reports	https://quickstats.nass.usda.gov/
Climate datasets	Links
gridMET	https://www.climatologylab.org/gridmet.html

Table B.2. Likelihood ratio test between models with and without HD.

Simulated Likelihood Ratio Test: 1,000 replications			
Model	AIC	BIC	p-value
Without HD	74,485	74,624	
With HD	74,300	74,446	<0.001

Table B.3. Coefficient estimates from modelling regression.

Climate indices	Coefficients	SEs	p-values
Prcp _{p1} (50 mm)	0.312	0.052	<0.001
Prcp _{p2} (50 mm)	0.583	0.063	<0.001
Prcp _{p3} (50 mm)	0.060	0.062	0.338
Prcp _{p1} Squared (50 ² mm)	-0.025	0.005	<0.001
Prcp _{p2} Squared (50 ² mm)	-0.110	0.014	<0.001
Prcp _{p3} Squared (50 ² mm)	-0.013	0.008	0.119
GDD _{p1} (100°C days)	0.027	0.014	0.050
GDD _{p2} (100°C days)	0.006	0.052	0.902
GDD _{p3} (100°C days)	0.062	0.024	0.009
FDD _{p1} (1°C day)	-0.001	0.000	<0.001
FDD _{p2} (1°C day)	-0.090	0.018	<0.001
EDD _{p2} (1°C day)	-0.072	0.031	0.020
EDD _{p3} (1°C day)	-0.022	0.011	0.052
HD _{p3} (1%)	-0.010	0.002	<0.001
Observations	25,359		
R-squared	0.41		
p-value (F-test)	<0.001		

Notes: Specific phenological periods: planting to jointing (p1), jointing to heading (p2), and heading to maturity (p3) periods. The p-values were estimated by the clustered standard errors (SEs) by cultivar and year.

Table B.4. Cultivar-specific information, average sensitivity to hot-dry events (t ha⁻¹ per % HD), and average simulated yields (t ha⁻¹) across 500 bootstrap samples, and the proportion (%) of 500 bootstrap samples corresponding to each category.

Cultivars	Release years	No. of observations	Cultivar source	Average HD sensitivity	Average simulated yields	HyHt (%)	LyHt (%)	HyHs (%)	LyHs (%)
Hawk	1981	71	Company	-0.001	2.99	7.6	81.0	0.0	11.4
Sandy	1981	75	Colorado	-0.006	2.88	0.0	77.2	0.0	22.8
Brule	1982	149	Nebraska	-0.001	3.04	4.4	93.6	0.0	2.0
Centura	1983	199	Nebraska	-0.004	2.93	0.0	91.8	0.0	8.2
Colt	1984	136	Nebraska	-0.003	3.00	0.2	95.4	0.0	4.4
Siouxland	1984	243	Nebraska	-0.003	3.02	0.6	97.8	0.0	1.6
TAM 107	1984	386	Taxes	-0.003	3.05	0.8	98.8	0.0	0.4
Thunderbird	1985	189	Company	-0.008	2.97	0.4	76.4	0.0	23.2
Cody	1986	75	Nebraska	-0.002	2.99	1.2	96.0	0.0	2.8
Norkan	1986	99	Kansas	-0.004	2.89	0.2	89.4	0.0	10.4
TAM 200	1986	153	Taxes	0.001	3.01	1.2	97.2	0.0	1.6
Abilene	1988	137	Company	-0.006	3.10	15.2	69.6	1.2	14.0
Arapahoe	1988	447	Nebraska	-0.005	3.08	1.0	96.6	0.0	2.4
Karl	1988	129	Kansas	-0.012	2.99	2.8	36.4	0.0	60.8
Lamar	1988	92	Colorado	-0.002	2.93	0.4	94.4	0.0	5.2
Redland	1988	163	Nebraska	-0.003	3.10	10.0	85.2	0.0	4.8
Longhorn	1990	91	Company	-0.003	2.85	0.0	91.8	0.0	8.2
Tomahawk	1990	116	Company	-0.008	3.06	14.8	44.0	0.8	40.4
Laredo	1991	67	Company	-0.008	3.00	3.0	63.6	0.8	32.6
Yuma	1991	149	Colorado	-0.010	3.00	0.6	53.2	1.2	45.0
Karl 92	1992	179	Kansas	-0.007	3.04	3.6	75.0	0.0	21.4
Ogallala	1992	107	Company	-0.012	3.06	5.4	36.2	3.6	54.8
Vista	1992	194	Nebraska	-0.006	3.05	2.0	86.0	0.0	12.0
Akron	1994	241	Colorado	-0.008	3.03	0.4	73.4	0.0	26.2
Alliance	1994	398	Company	-0.011	3.13	8.2	36.4	8.8	46.6
Coronado	1994	109	Company	0.002	3.24	76.0	24.0	0.0	0.0
Halt	1994	196	Colorado	-0.007	3.01	0.6	78.4	0.0	21.0
Jagger	1994	624	Kansas	-0.003	3.03	0.0	100.0	0.0	0.0
Jules	1994	69	Colorado	-0.012	2.98	1.0	39.6	0.6	58.8
Nekota	1994	99	Nebraska	-0.003	3.03	4.0	82.2	0.0	13.8
Niobrara	1994	132	Nebraska	-0.004	3.11	15.2	75.8	1.2	7.8
2137	1995	389	Kansas	-0.008	3.18	41.8	44.4	4.2	9.6
AP7510	1995	63	Company	-0.024	3.25	3.2	0.0	68.6	28.2
T81	1995	61	Company	-0.008	3.23	42.0	16.0	27.8	14.2
Century	1996	72	Oklahoma	-0.011	2.96	3.8	43.4	0.6	52.2
TAM 110	1996	131	Taxes	-0.006	3.07	5.4	82.8	0.6	11.2
2174	1997	146	Oklahoma	-0.007	2.99	0.4	75.2	0.0	24.4
Windstar	1997	99	Nebraska	-0.006	3.08	11.2	66.6	1.8	20.4

Table B.4. Continued.

Cultivars	Release years	No. of observations	Cultivar source	Average HD sensitivity	Average simulated yields	HyHt (%)	LyHt (%)	HyHs (%)	LyHs (%)
Yumar	1997	93	Colorado	-0.018	2.92	0.0	7.6	0.6	91.8
Enhancer	1998	96	Company	-0.014	2.96	0.0	23.2	0.0	76.8
Onaga	1998	70	Company	-0.003	3.13	34.6	38.0	0.2	27.2
Prowers	1998	61	Colorado	-0.016	2.81	0.0	25.8	0.0	74.2
Culver	1999	118	Nebraska	-0.006	3.06	6.8	73.8	0.6	18.8
Kalvesta	1999	55	Company	-0.016	2.98	0.2	13.8	1.2	84.8
Nuplains	1999	76	Nebraska	-0.002	2.92	0.0	94.6	0.0	5.4
Prairie Red	1999	197	Colorado	-0.010	3.06	1.8	55.4	1.8	41.0
Prowers 99	1999	72	Colorado	-0.015	2.63	0.0	16.0	0.0	84.0
Thunderbolt	1999	97	Company	-0.006	3.05	3.8	75.6	0.2	20.4
Trego	1999	178	Kansas	-0.009	3.13	12.2	48.4	8.0	31.4
Wesley	1999	467	Nebraska	-0.009	3.19	41.6	30.0	14.0	14.4
Lakin	2000	89	Kansas	-0.011	2.87	0.0	47.2	0.0	52.8
Millennium	2000	299	Nebraska	-0.007	3.30	80.8	1.8	16.8	0.6
NuFrontier	2000	115	Company	-0.010	3.07	3.0	48.6	2.2	46.2
NuHorizon	2000	61	Company	-0.009	2.97	2.6	57.8	0.2	39.4
Stanton	2000	93	Kansas	-0.015	2.92	0.0	19.0	0.2	80.8
Venango	2000	64	Company	-0.020	2.94	0.0	1.4	0.4	98.2
2145	2001	185	Kansas	-0.008	3.13	18.8	50.2	3.6	27.4
AP502CL	2001	115	Company	-0.002	2.92	0.0	95.2	0.0	4.8
Above	2001	207	Colorado	-0.007	3.06	3.0	80.4	2.0	14.6
Ankor	2001	97	Oklahoma	-0.015	2.97	0.0	16.8	0.8	82.4
Avalanche	2001	125	Colorado	-0.011	2.98	0.0	42.8	0.4	56.8
Cutter	2001	120	Company	-0.002	3.30	84.6	10.4	4.6	0.4
Jagalene	2001	467	Company	-0.003	3.09	4.0	95.8	0.0	0.2
Wahoo	2001	192	Nebraska	-0.001	3.29	93.6	6.0	0.4	0.0
Goodstreak	2002	206	Nebraska	-0.014	3.01	0.0	16.2	0.4	83.4
Harry	2002	103	Nebraska	-0.007	3.23	52.8	20.0	16.2	11.0
Overley	2003	250	Kansas	-0.001	3.24	78.4	20.8	0.6	0.2
Santa Fe	2003	250	Company	-0.006	3.24	72.4	18.0	7.2	2.4
TAM 111	2003	374	Taxes	-0.012	3.19	14.0	15.6	40.8	29.6
Deliver	2004	210	Oklahoma	-0.009	3.12	10.6	50.8	5.6	33.0
Endurance	2004	396	Oklahoma	-0.015	3.20	2.8	2.8	60.0	34.4
Hatcher	2004	322	Colorado	-0.012	3.27	34.0	3.8	57.6	4.6
Sturdy 2K	2004	81	Taxes	0.004	3.23	69.6	29.8	0.0	0.6
Bond CL	2005	168	Colorado	-0.015	3.22	8.2	3.0	61.8	27.0
Danby	2005	69	Kansas	-0.017	3.16	4.6	7.8	40.8	46.8
Infinity CL	2005	217	Nebraska	-0.008	3.22	49.6	22.6	21.0	6.8
Keota	2005	108	Company	-0.012	3.08	3.8	35.6	7.8	52.8
OK Bullet	2005	168	Oklahoma	-0.002	3.03	1.6	92.8	0.0	5.6
Okfield	2005	55	Oklahoma	0.007	3.00	10.0	88.8	0.0	1.2

Table B.4. Continued.

Cultivars	Release years	No. of observations	Cultivar source	Average HD sensitivity	Average simulated yields	HyHt (%)	LyHt (%)	HyHs (%)	LyHs (%)
TAM 112	2005	329	Taxes	-0.007	3.24	71.8	17.4	9.2	1.6
Centerfield	2006	98	Oklahoma	-0.005	2.93	0.0	81.4	0.0	18.6
Duster	2006	414	Oklahoma	-0.009	3.22	46.2	18.2	26.6	9.0
Fuller	2006	360	Kansas	-0.008	3.16	29.4	51.8	7.0	11.8
NuDakota	2006	66	Company	-0.014	3.30	21.4	2.2	64.8	11.6
NuGrain	2006	60	Company	-0.015	3.03	2.2	19.0	6.8	72.0
Post Rock	2006	113	Company	-0.010	3.06	3.2	49.2	3.4	44.2
Shocker	2006	146	Company	-0.003	3.12	22.4	69.4	0.6	7.6
Art	2007	176	Company	0.003	3.26	80.2	19.6	0.2	0.0
Bill Brown	2007	140	Colorado	-0.018	3.21	0.6	1.4	58.0	40.0
Doans	2007	185	Company	-0.014	3.06	1.4	18.2	1.2	79.2
Overland	2007	314	Nebraska	-0.006	3.44	82.6	0.0	17.4	0.0
Ripper	2007	137	Colorado	-0.007	3.21	44.4	25.4	19.0	11.2
TAM 203	2007	107	Taxes	-0.014	3.32	22.0	0.8	74.2	3.0
TAM 304	2007	174	Taxes	-0.008	3.37	77.0	0.2	22.6	0.2
Winterhawk	2007	384	Company	-0.011	3.34	45.0	0.2	54.4	0.4
Armour	2008	283	Company	-0.005	3.20	57.0	35.6	4.4	3.0
Camelot	2008	202	Nebraska	-0.003	3.20	56.6	39.0	3.0	1.4
Jackpot	2008	226	Company	-0.009	3.23	46.8	14.8	29.6	8.8
Settler CL	2008	282	Nebraska	-0.006	3.31	84.0	2.0	13.2	0.8
TAM 401	2008	119	Taxes	-0.011	3.13	6.6	35.6	16.0	41.8
Thunder CL	2008	81	Colorado	-0.012	3.10	4.0	26.2	13.0	56.8
Billings	2009	197	Oklahoma	-0.016	3.22	7.8	3.0	60.0	29.2
Everest	2009	270	Kansas	-0.012	3.28	32.4	3.0	59.6	5.0
Snowmass	2009	141	Colorado	-0.018	3.46	6.2	0.0	93.4	0.4
T158	2009	301	Company	-0.012	3.27	28.6	6.0	59.0	6.4
CJ	2010	75	Company	-0.014	3.18	19.2	10.4	31.4	39.0
Greer	2010	182	Company	-0.012	3.26	32.8	6.0	53.4	7.8
McGill	2010	137	Nebraska	-0.007	3.24	53.8	18.4	21.2	6.6
Robidoux	2010	173	Nebraska	-0.01	3.20	28.4	20.2	30.2	21.2
T154	2010	60	Company	-0.013	3.30	28.4	7.0	56.8	7.8
Brawl CL Plus	2011	200	Colorado	-0.015	3.36	11.8	1.0	85.6	1.6
Byrd	2011	219	Colorado	-0.015	3.57	17.8	0.0	82.2	0.0
Denali	2011	206	Colorado	-0.018	3.51	2.0	0.0	98.0	0.0
Garrison	2011	132	Oklahoma	-0.012	3.15	13.4	27.0	21.4	38.2
Ruby Lee	2011	236	Oklahoma	-0.017	3.24	4.0	0.6	76.8	18.6
SY Wolf	2011	311	Company	-0.013	3.55	26.6	0.0	73.4	0.0
T153	2011	55	Company	-0.018	3.28	9.2	3.8	72.6	14.4
TAM 113	2011	129	Taxes	-0.011	3.16	15.2	30.6	23.2	31.0

Table B.4. Continued.

Cultivars	Release years	No. of observations	Cultivar source	Average HD sensitivity	Average simulated yields	HyHt (%)	LyHt (%)	HyHs (%)	LyHs (%)
WB-Cedar	2011	243	Company	-0.009	3.38	62.4	0.2	37.2	0.2
1863	2012	88	Kansas	-0.027	3.16	0.0	0.0	40.0	60.0
Gallagher	2012	279	Oklahoma	-0.023	3.38	0.0	0.0	99.8	0.2
Iba	2012	254	Oklahoma	-0.022	3.34	0.2	0.0	99.0	0.8
LCS Mint	2012	363	Colorado	-0.008	3.34	75.4	1.0	23.4	0.2
SY Southwind	2012	79	Company	-0.002	3.29	73.8	12.6	9.0	4.6
WB-Grainfield	2012	415	Company	-0.021	3.50	0.0	0.0	100.0	0.0
LCS Wizard	2013	110	Colorado	-0.010	2.94	1.2	54.2	0.2	44.4
Oakley CL	2013	91	Kansas	-0.023	3.89	1.8	0.0	98.2	0.0
WB4458	2013	213	Company	-0.016	3.35	11.8	0.6	85.0	2.6
Kan Mark	2014	86	Kansas	0.002	3.33	80.6	9.8	5.6	4.0
SY Monument	2014	306	Company	-0.024	3.62	0.0	0.0	100.0	0.0
TAM 114	2014	170	Texas	-0.022	3.54	0.6	0.0	99.4	0.0
TAM 204	2014	153	Texas	-0.011	3.22	31.6	13.4	35.8	19.2
Bentley	2015	140	Oklahoma	-0.017	3.32	11.8	0.4	77.4	10.4
Joe	2015	60	Kansas	-0.015	3.97	26.2	0.0	73.8	0.0
LCS Pistol	2015	118	Colorado	-0.011	3.14	20.8	28.4	14.4	36.4
SY Flint	2015	115	Company	-0.012	3.17	28.0	12.8	18.6	40.6
Antero	2016	112	Colorado	-0.018	3.89	11.8	0.0	88.2	0.0
Avery	2016	134	Colorado	-0.009	3.53	59.0	0.0	41.0	0.0
LCS Chrome	2016	184	Colorado	-0.023	3.43	0.2	0.0	99.6	0.2
Larry	2016	71	Kansas	-0.023	3.18	5.4	1.2	46.0	47.4
Bob Dole	2017	60	Kansas	-0.042	3.27	0.0	0.0	72.6	27.4
LCS Link	2017	62	Colorado	-0.024	3.61	5.0	0.0	94.4	0.6
SY 517 CL2	2017	58	Company	-0.028	3.03	0.2	0.2	8.2	91.4
SY Grit	2017	94	Company	-0.017	3.04	4.0	15.6	7.4	73.0
Tatanka	2017	56	Kansas	-0.023	3.78	7.2	0.0	92.6	0.2
WB4269	2017	80	Company	-0.002	3.61	76.4	0.0	23.4	0.2
WB4303	2017	77	Company	-0.011	3.45	47.8	0.0	47.6	4.6
WB4721	2017	94	Company	-0.020	3.48	4.0	0.0	95.2	0.8
Langin	2018	170	Colorado	-0.021	3.83	1.8	0.0	98.2	0.0
SY Rugged	2018	143	Company	-0.017	3.39	9.6	0.4	88.2	1.8

Notes: Four categories: high yield potential and HD-tolerant (HyHt; yellow), low yield potential and HD-tolerant (LyHt; green), high yield potential and HD-sensitive (HyHs; blue), and low yield potential and HD-sensitive (LyHs; purple). The cultivar-specific color indicates the main characteristic with the largest proportion.

Table B.5. Prediction accuracy for the preferred and alternative models.

Model	rmse
M1: Preferred	1.035
M2: Preferred model + interaction terms of EDD _{p3} with cultivars	1.042
M3: Preferred model + interaction terms of all other climatic variables with cultivars	1.092
M4: Same as M1 but replacing temperature indices with Tavg and Tavg ²	1.042
M5: Same as M3 but replacing temperature indices with Tavg and Tavg ²	1.050

Notes: The preferred model (M1) allows the effect of HD during heading to maturity period (p3) to vary across cultivars. The second model (M2) allows the effects of extreme degree days (EDD) and HD during p3 to vary across cultivars, and the third model (M3) allows the effects of all climate indices to vary across cultivars. Additionally, we also replaced growing degree days (GDD), freezing degree days (FDD), and EDD during specific phenological periods with average temperature (Tavg) and a quadratic term (Tavg²) during three phenological periods to estimate the HD sensitivity by allowing the effects of HD (M4) or all climate variables (M5) to vary across cultivars. Each model is run 100 times, with each iteration using a random selection of 80 percent of the 25,359 observations. Parameter estimates are then used to predict yields for the omitted 20 percent in each subsample. The average root-mean-squared-errors (rmse) are reported for these predictions. The smaller the rmse, the better the performance of the model.

Table B.6. Dataset subsets used for different analyses. All subsets are derived from the full dataset (25,359 observations across 150 winter wheat cultivars and multiple site-years). Each subset was selected to address specific research questions.

Analysis Objective	Dataset Subset	Purpose	Figure
Breeding-driven yield trends across environments	58 balanced cultivar × environment groups	Ensure comparability across environments	Figure 3.2a
Case study based on reference cultivar	438 site-years (where ‘Arapahoe’ was grown)	Compare yield trends under favorable/adverse conditions	Figure 3.2b
Temporal changes in HD resilience	435 groups (derived from full dataset, based on release-year window)	Regression for each group to show temporal changes in HD resilience	Figure 3.3a

Supplementary References

1. Zhao, H., *et al.* US winter wheat yield loss attributed to compound hot-dry-windy events. *Nat. Commun.* **13**, 1-9 (2022).
2. Peairs, F. & Armenta, R. *Wheat Production and Pest Management for the Great Plains Region*. (Colorado State University Extension, 2010).
3. Sacks, W. J. & Kucharik, C. J. Crop management and phenology trends in the US Corn Belt: Impacts on yields, evapotranspiration and energy balance. *Agric. For. Meteorol.* **151**, 882-894 (2011).
4. Tollenaar, M., Fridgen, J., Tyagi, P., Stackhouse Jr, P. W. & Kumudini, S. The contribution of solar brightening to the US maize yield trend. *Nat. Clim. Change* **7**, 275-278 (2017).
5. Robertson, L. D., Guy, S. O. & Brown, B. D. *Southern Idaho Dryland Winter Wheat Production Guide*. (University of Idaho: Moscow, ID, USA, 2004).
6. Zaveri, E. & Lobell, D. The role of irrigation in changing wheat yields and heat sensitivity in India. *Nat. Commun.* **10**, 1-7 (2019).
7. Cesaraccio, C., Spano, D., Duce, P. & Snyder, R. L. An improved model for determining degree-day values from daily temperature data. *Int. J. Biometeorol.* **45**, 161-169 (2001).
8. Warrick, B. E. & Miller, T. D. *Freeze Injury on Wheat*. (Texas Agricultural Extension Service The Texas A and M University System, San Angelo, Texas, 1999).
9. Tack, J., Barkley, A., & Nalley, L. L. Effect of warming temperatures on US wheat yields. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 6931-6936 (2015).
10. Zhang, T., He, Y., DePauw, R., Jin, Z., Garvin, D., Yue, X., ... & Yang, X. Climate change may outpace current wheat breeding yield improvements in North America. *Nat. Commun.*, **13**, 1-9 (2022).
11. Kahiluoto, H., Kaseva, J., Balek, J., Olesen, J. E., Ruiz-Ramos, M., Gobin, A., ... & Trnka, M. Decline in climate resilience of European wheat. *Proc. Natl. Acad. Sci. U.S.A.* **116**, 123-128 (2019).
12. Shew, A. M., Tack, J. B., Nalley, L. L., & Chaminuka, P. Yield reduction under climate warming varies among wheat cultivars in South Africa. *Nat. Commun.* **11**, 1-9 (2020).
13. Xiong, W., Reynolds, M. P., Crossa, J., Schulthess, U., Sonder, K., Montes, C., ... & Payne, T. Increased ranking change in wheat breeding under climate change. *Nat. Plants*, **7**, 1207-1212 (2021).
14. Boiko, O., Kagone, S., & Senay, G. (2021). Soil properties dataset in the United States. *USGS Data Release*.

Appendix C - Supplemental Information for Chapter 4

Text C.1 Calculation of GDD, FDD, and EDD

We calculated growing degree days (GDD, °C days), freeze degree days (FDD, °C days) and extreme degree days (EDD, °C days), as follows:

$$GDD = \sum_{d=1}^D (T_d^{adjusted} - T_{base}) \quad T_{base} = 0^{\circ}\text{C} \quad (\text{S1})$$

$$FDD = \sum_{h=1}^H DD_h \quad DD_h = \begin{cases} 0 & \text{if } T_h \geq T_{low} \\ \frac{|T_h - T_{low}|}{24} & \text{if } T_h < T_{low} \end{cases} \quad (\text{S2})$$

$$EDD = \sum_{h=1}^H DD_h \quad DD_h = \begin{cases} 0 & \text{if } T_h < T_{high} \\ \frac{(T_h - T_{high})}{24} & \text{if } T_h \geq T_{high} \end{cases} \quad (\text{S3})$$

where $T_d^{adjusted}$ is the adjusted mean temperature (°C) on day d , which is calculated by (1) imposing a maximum of 30°C and a minimum of 0°C on the daily minimum and maximum temperatures, and (2) taking the average of these adjusted minimum and maximum temperatures¹. T_{base} is the base temperature for winter wheat (0°C). D is the number of days. T_h is the simulated hourly temperature derived from daily maximum and minimum temperatures². DD_h represents degree days for hour h , and H is the number of hours. T_{low} is the cold stress threshold (-11°C and 0°C during p1 and p2 periods, respectively)^{3,4}, while T_{high} denotes the heat stress threshold (30°C during p2 and p3 periods)⁵.

Text C.2 Quantifying the impact of climate trends with a fixed growing season

Following the approach of previous studies^{6,7}, we used the winter wheat calendar developed by Sacks et al. (2010)⁸, which provides planting and harvest dates at a 0.5° resolution

around the year 2000 (Table C.1), to obtain location-specific planting and harvest dates from the nearest grid. For each of the 1,101 site-years included in our preferred model (Eq. 2 in Main Text), we calculated the climate variables including mean temperature (Tm , °C) and total precipitation (P , mm) during the entire growing season. We then modified our model (Eq. 2 in Main Text) by replacing the original climate variables with the following specification:

$$(fW_{l,t}; \beta_{var}) = \beta_1 Tm_{l,t} + \beta_2 Tm_{l,t}^2 + \beta_3 P_{l,t} + \beta_4 P_{l,t}^2 \quad (S4)$$

where $f(W_{l,t}; \beta_{var})$ represents the effects of climate variables with their corresponding coefficients β . Here, “ l ” and “ t ” denote specific locations and years, respectively. Quadratic terms (Tm^2 and P^2) were included to capture nonlinear responses (Table C.3). Finally, for the 12 long-term trial sites, we quantified the impact of climate trends under the fixed growing season framework using the same procedure described in the Main Text but applying Eq. S4.

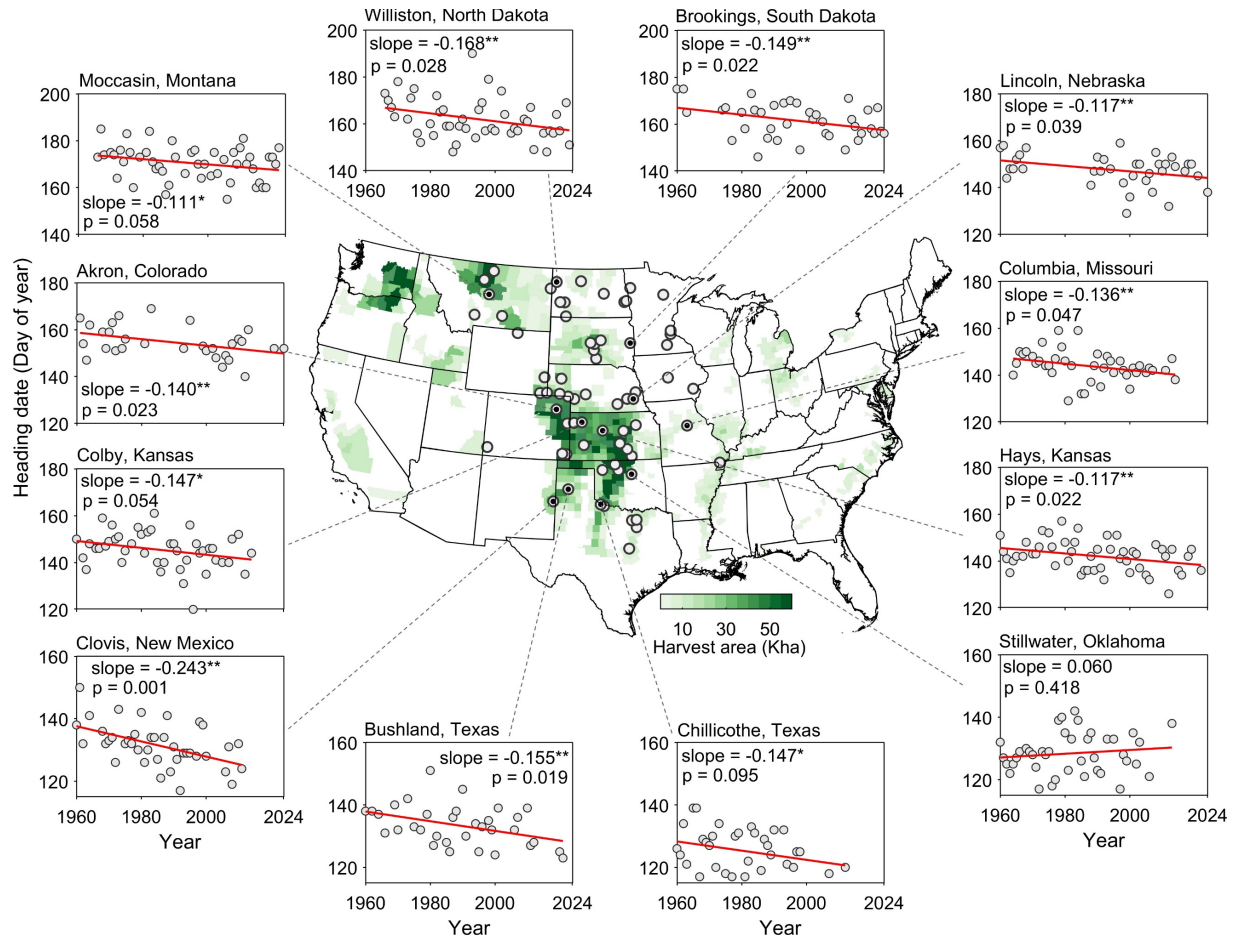


Figure C.1. Time series of winter wheat heading dates at 12 trial sites. The map shows all trial sites compiled in this study (circles) and the 12 long-term trial sites (black dots). Background shading represents the county-level average harvested area of winter wheat in the U.S. during 2001-2020, based on USDA-NASS data. Surrounding panels show observed time series of heading dates at the 12 long-term sites. Red lines represent the linear regression trends, with “*” and “**” indicating p-value < 0.1 and p-value < 0.05, respectively.

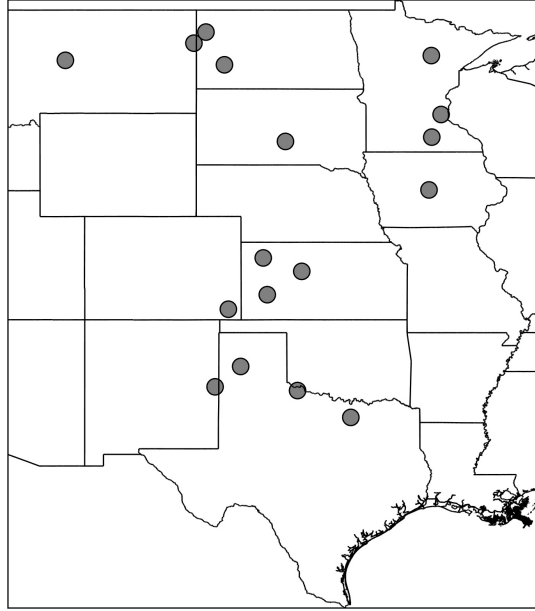


Figure C.2. Spatial distribution of sites with observed maturity dates.

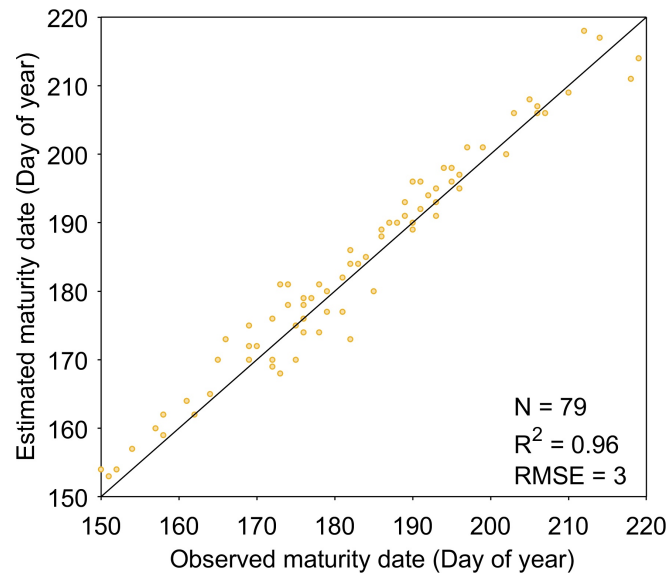


Figure C.3. Performance of maturity date estimations. Scatterplot comparing observed versus estimated maturity dates across all available site-years ($N = 79$). The black line indicates the 1:1 line.

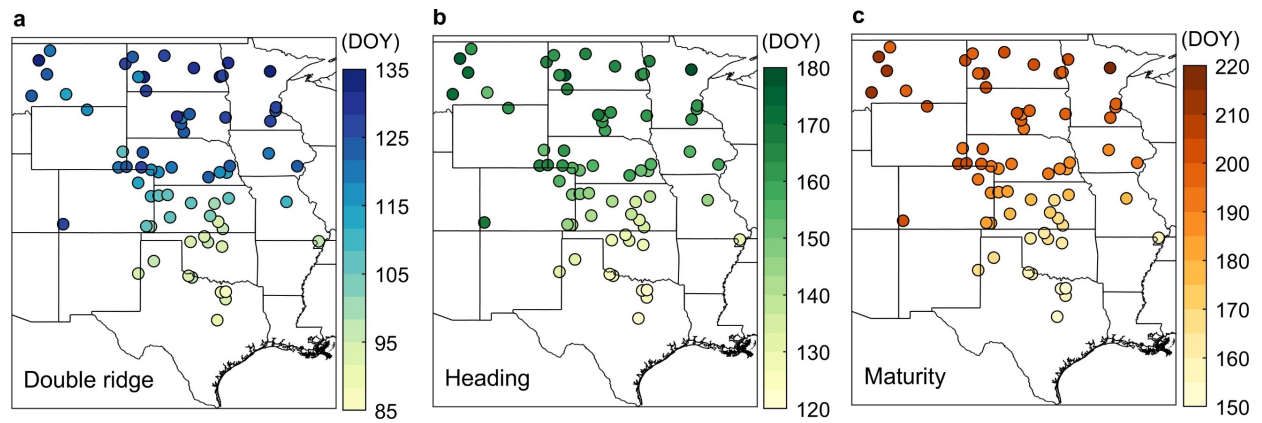


Figure C.4. Average phenology (days of year, DOY) for sites included in our dataset. a-c, Estimated double ridge (a) and maturity dates (c), and observed heading dates (b) across trial years in our dataset.

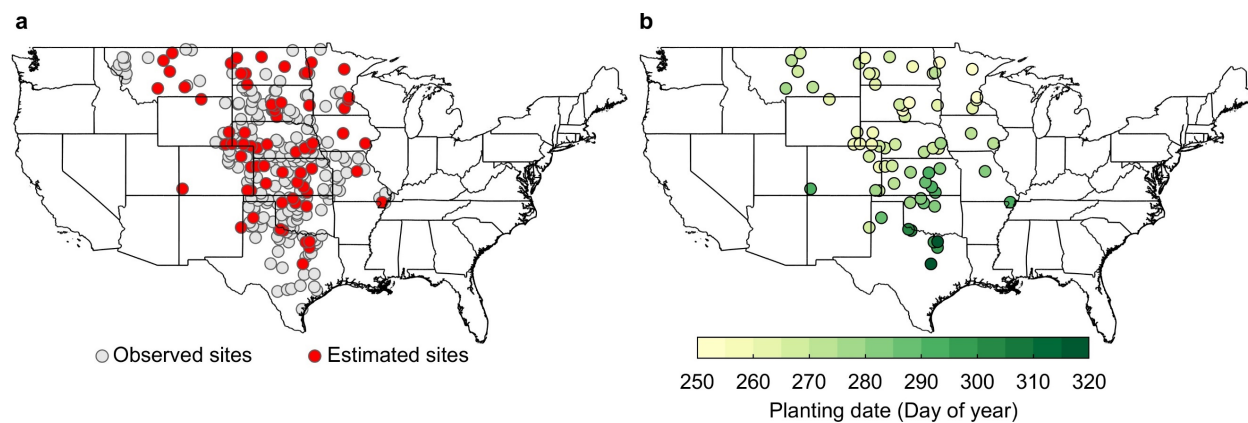


Figure C.5. Spatial distribution of sites with observed planting dates. a, 296 sites with observed planting dates (gray) and 68 sites where planting dates needed to be estimated (red). b, Estimated average planting dates.

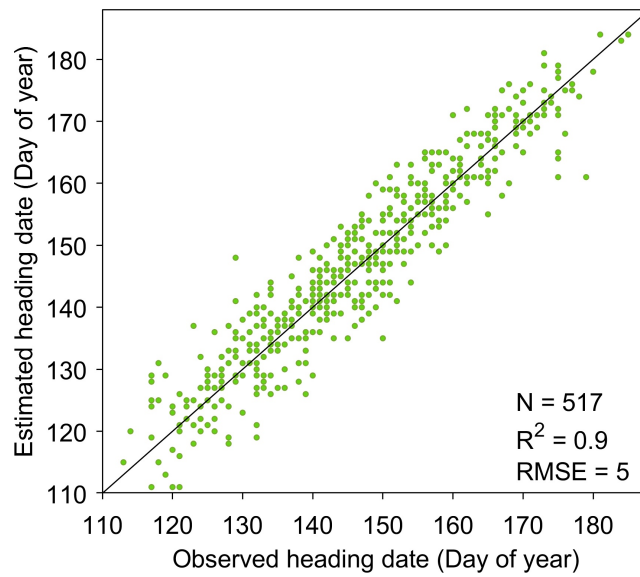


Figure C.6. Performance of heading date estimations. Scatterplot comparing observed versus estimated heading dates across all available years at the 12 long-term sites ($N = 517$). The black line indicates the 1:1 line.

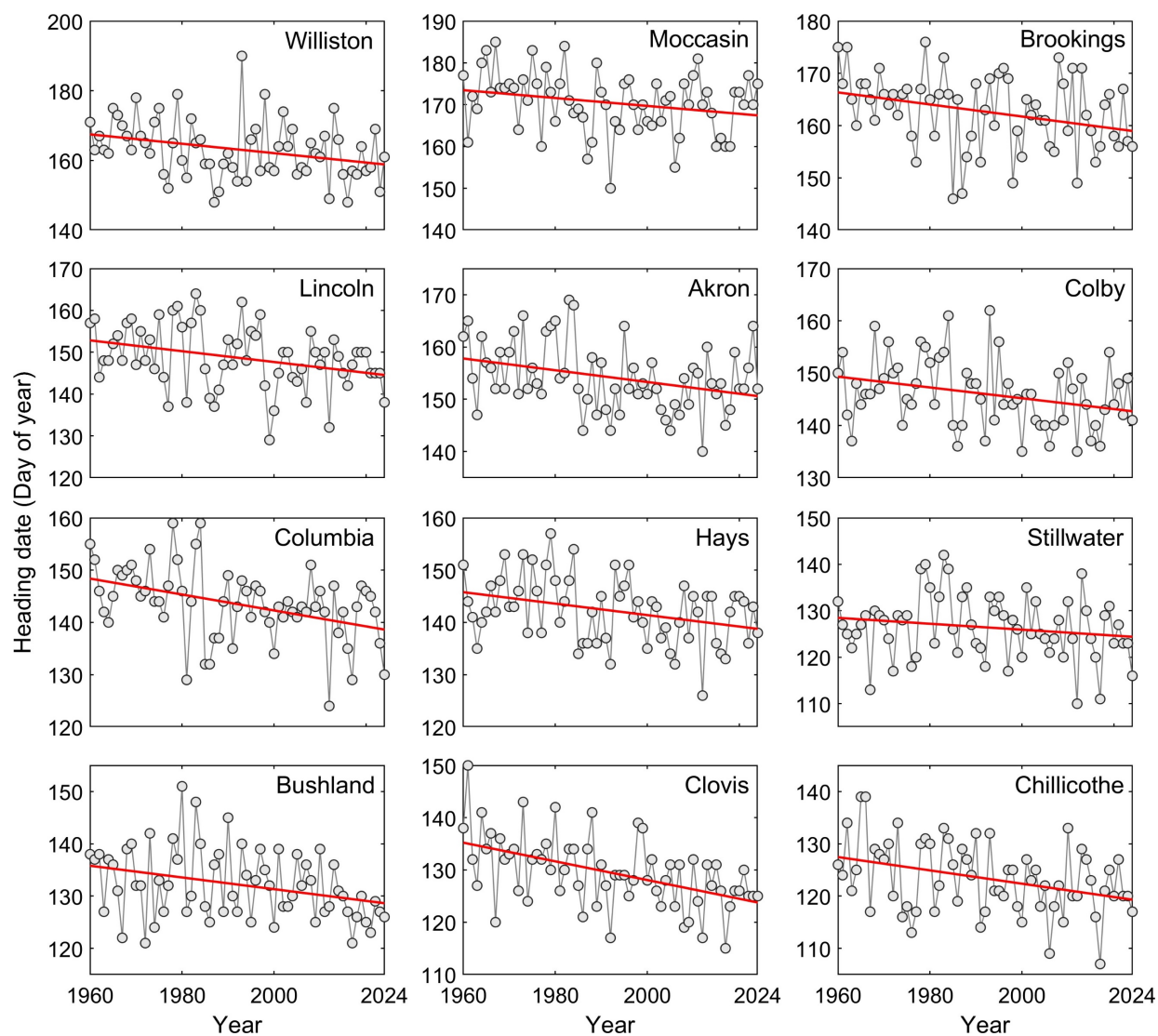


Figure C.7. Time series of heading dates at 12 sites from 1960 to 2024. Red lines represent the linear regression trends.

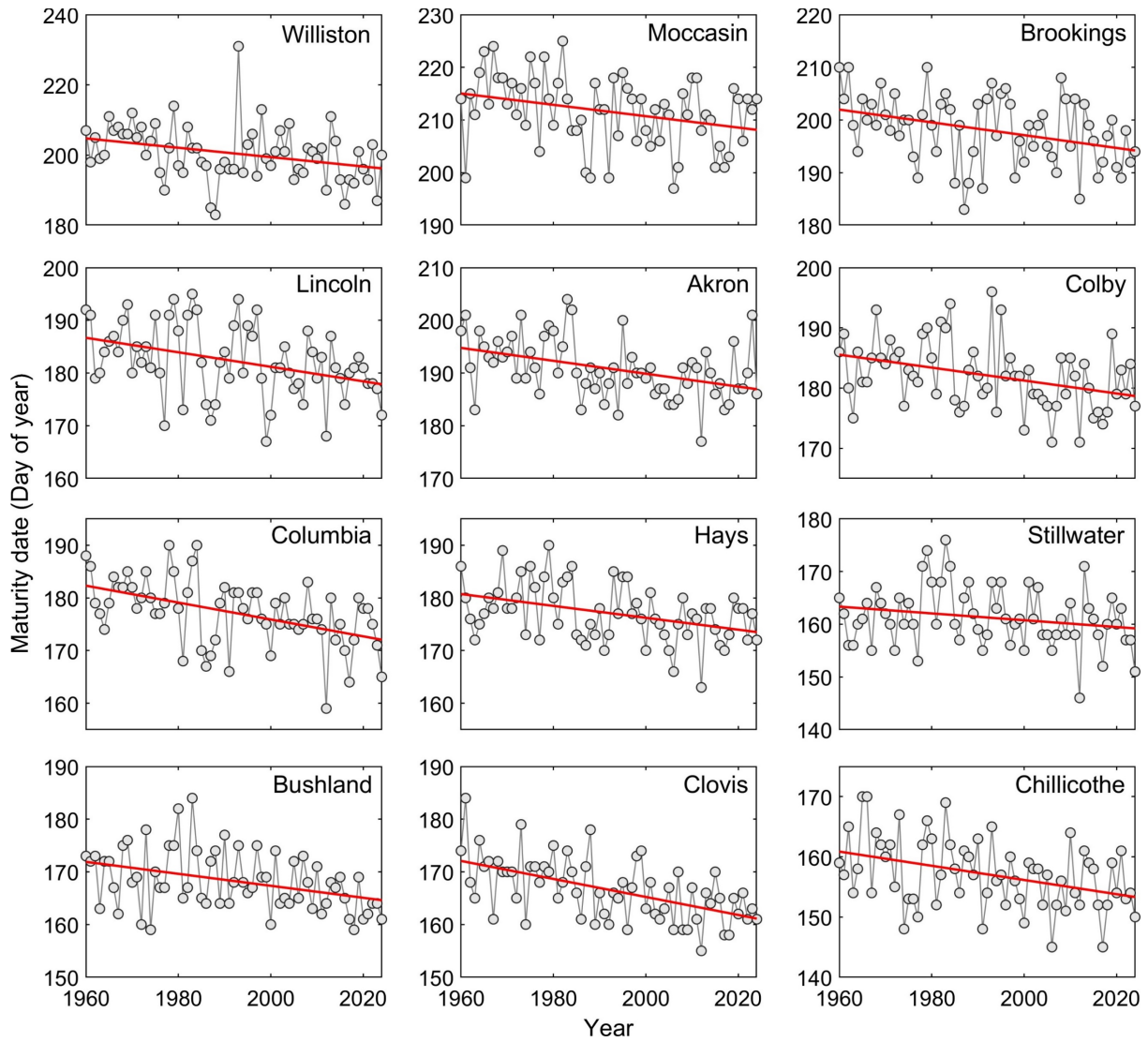


Figure C.8. Time series of maturity dates at 12 sites from 1960 to 2024. Red lines represent the linear regression trends.

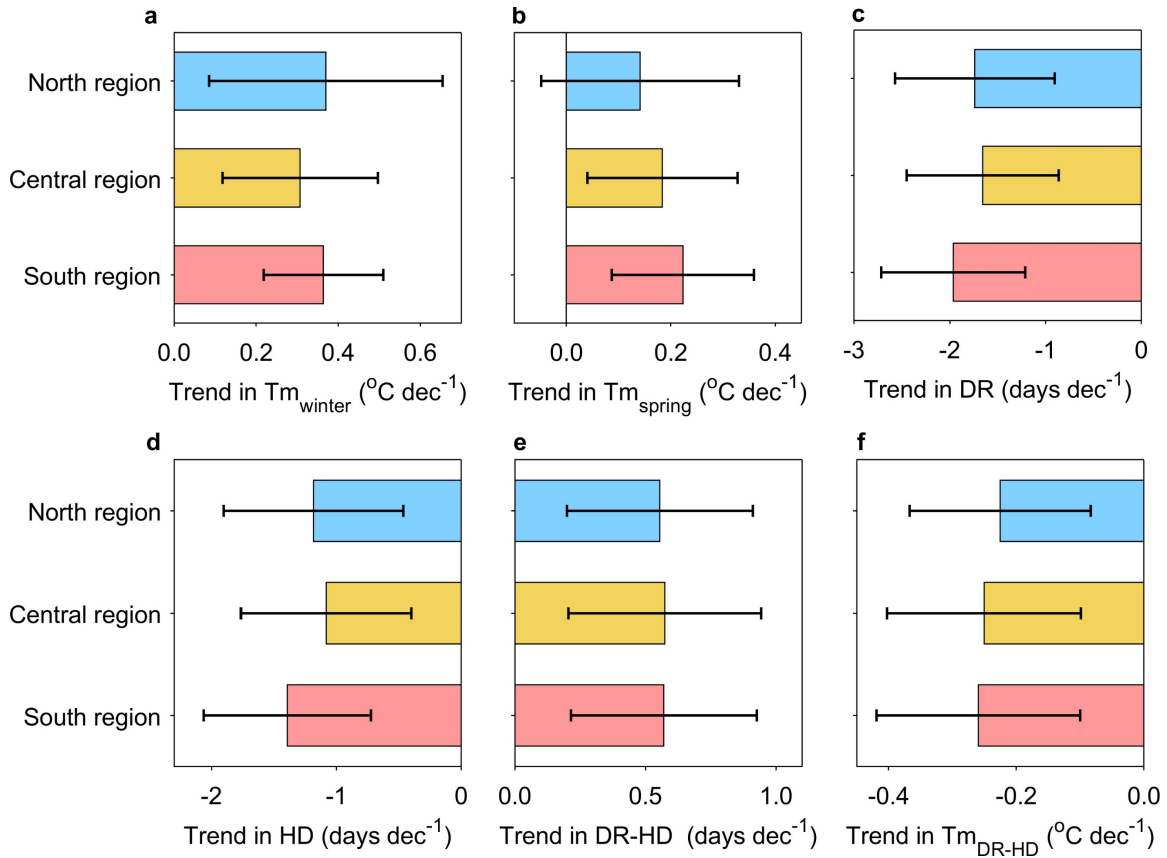


Figure C.9. Trend in temperature and phenology from 1960 to 2024 at three regions. a, Mean temperature (Tm) during winter (December-February). b, Tm during spring (March-May). c, Double ridge (DR) dates. d, Heading (HD) dates. e, Duration of the DR-HD phase. f, Tm during the DR-HD phase. Bars represent mean trend estimates, and error bars indicate the 95% confidence intervals.

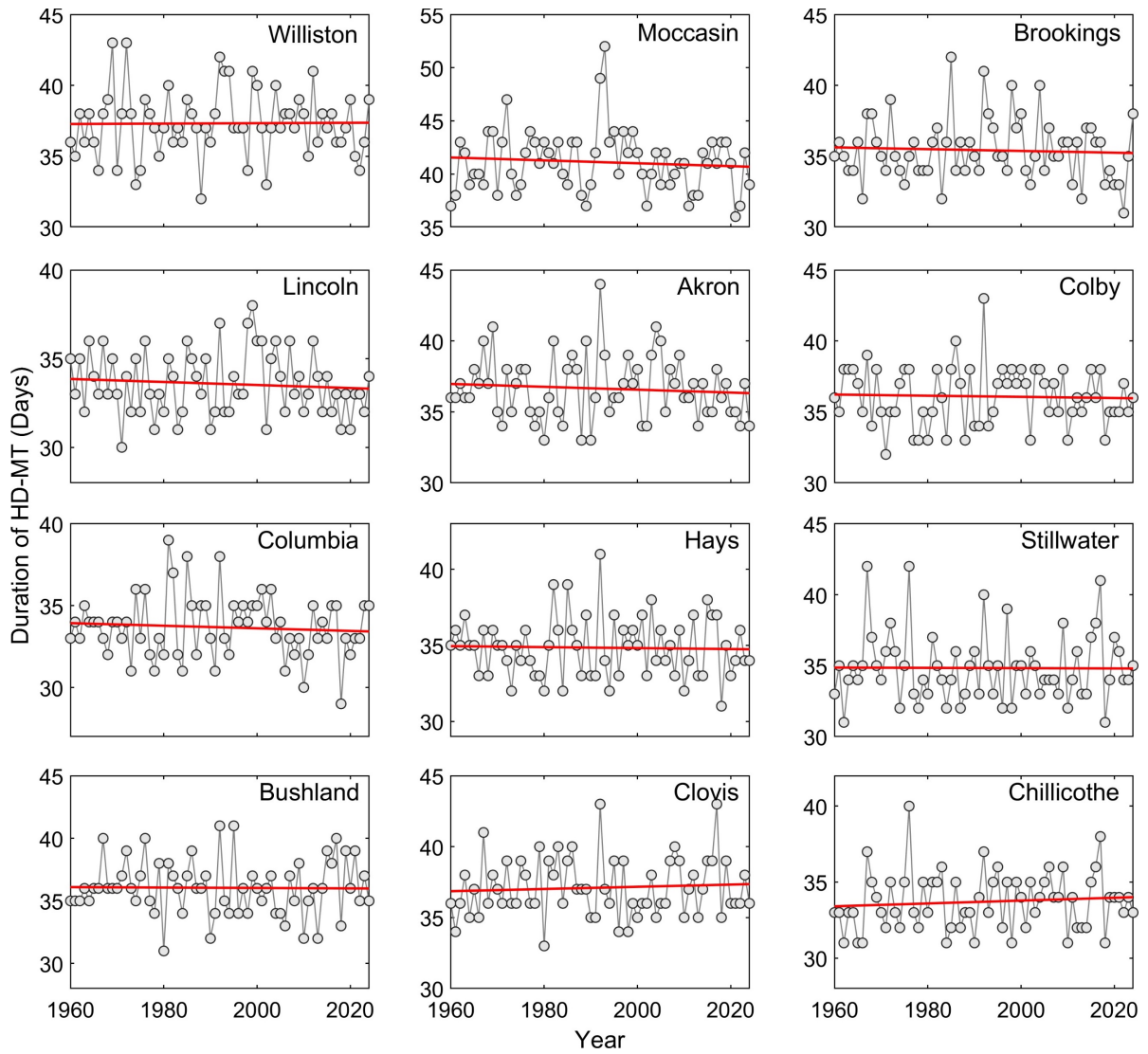


Figure C.10. Time series of duration from heading (HD) to maturity (MT) at 12 sites during 1960-2024. Red lines represent the linear regression trends.

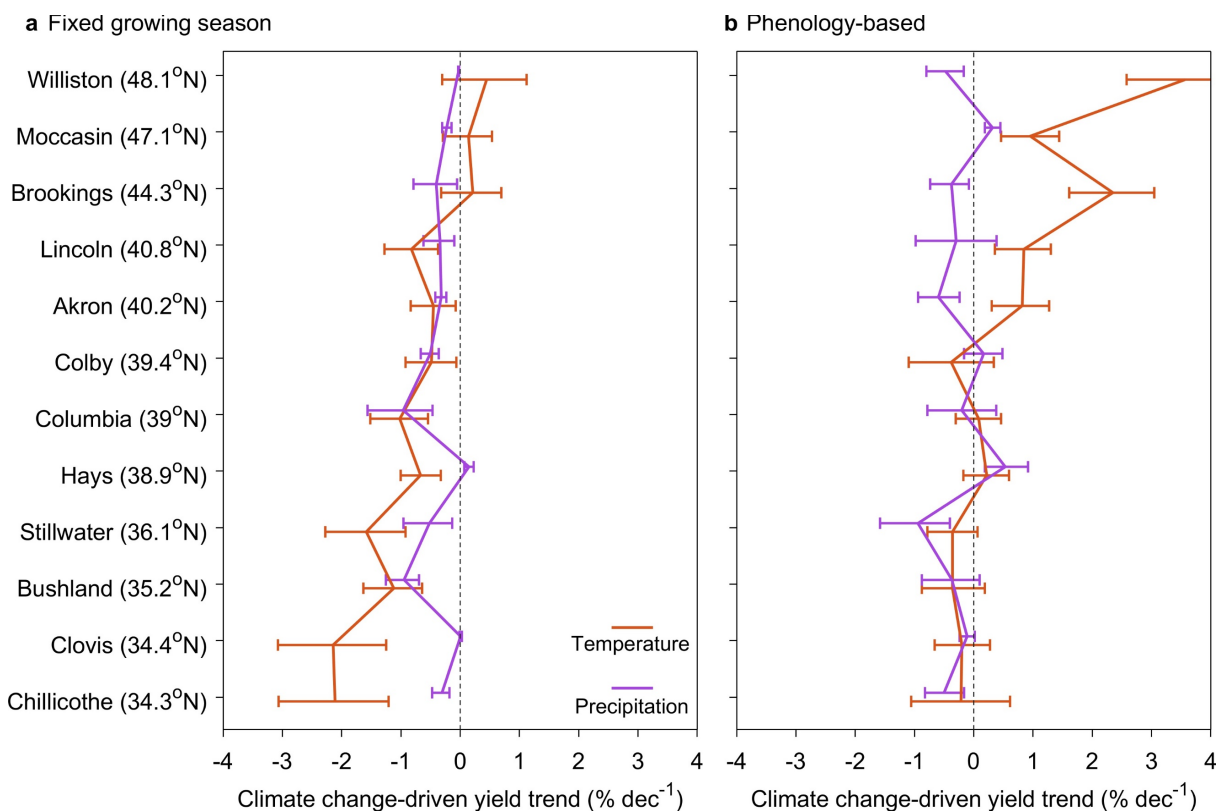


Figure C.11. Estimated impacts of temperature and precipitation trends from 1960 to 2024 at 12 sites using fixed growing season (a) and phenology-based (b) approaches. Values are expressed as a percentage of the average yield in our samples (2.3 t ha⁻¹). Error bars show the 2.5th-97.5th percentiles from 1,000 bootstrap replicates.

Table C.1. Links to public datasets for crop and climate data.

Datasets	Links
Yield and heading dates (USDA-ARS)	https://www.ars.usda.gov/plains-area/lincoln-ne/wheat-sorghum-and-forage-research/docs/hard-winter-wheat-regional-nursery-program/research/
Crop Calendar Dataset (Sacks et al., 2010)	https://sage.nelson.wisc.edu/data-and-models/datasets/crop-calendar-dataset/netcdf-0-5-degree/
Planting dates (Variety Test Reports)	Links
South Dakota	https://extension.sdstate.edu/winter-wheat-variety-trial-results https://openprairie.sdstate.edu
Nebraska	https://digitalcommons.unl.edu/extensionhist/ https://cropwatch.unl.edu/variety-testing/wheat/
Colorado	https://csucrops.org/winter-wheat/ https://archives.mountainscholar.org/digital/collection/p17393coll54/search
Kansas	https://www.ksre.k-state.edu/historicpublications/report-progress.html
Oklahoma	http://croptrials.okstate.edu/wheat/grain-yield https://digitalprairie.ok.gov/digital/collection/stgovpub/id/23998 https://www.okwheat.org/research-documents/variety-trials/ https://search.okstate.edu/?q=wheat+performance+test
Texas	https://varietytesting.tamu.edu/small-grains-archives/
North Dakota	https://www.ag.ndsu.edu/fss/variety-trials/winter-wheat/ https://www.ag.ndsu.edu/HettingerREC/archive/agronomy/
Montana	https://agresearch.montana.edu/nwarc/annual-reports/
Minnesota	https://varietytrials.umn.edu/winter-wheat
Wyoming	https://www.uwyo.edu/uwexpstn/research-results-impacts/variety-trials/wheat.html
Iowa	https://dr.lib.iastate.edu/search?query=winter%20wheat%20variety%202024&scope=76c07a07-0ef0-419f-a96a-1cadbca8fcb2 https://crops.extension.iastate.edu/post/2024-winter-wheat-variety-trial-results
Missouri	https://varietytesting.missouri.edu/archive.htm
New Mexico	https://clovissc.nmsu.edu/research/trials.html
Climate dataset	Link
NClimGrid-daily	https://www.ncei.noaa.gov/products/land-based-station/nclimgrid-daily

Notes: Kansas Variety Test Reports data from 1982-1994 were from printed documents that we digitized at the Department of Agronomy and Kansas Climate Center, Kansas State University.

Table C.2. Coefficient estimates from modelling regression.

Variables	Coefficients	CI	p-values
FDD _{p1} (°C day)	-0.0015	[-0.0022, -0.0007]	<0.001
FDD _{p2} (°C day)	-0.0220	[-0.0424, -0.0016]	0.0343
EDD _{p2} (°C day)	-0.0169	[-0.0651, 0.0313]	0.4926
EDD _{p3} (°C day)	-0.0176	[-0.0282, -0.0071]	0.0011
Prcp _{p1} (mm)	0.0030	[0.0004, 0.0056]	0.0214
Prcp _{p2} (mm)	0.0052	[0.0023, 0.0082]	<0.001
Prcp _{p3} (mm)	0.0011	[-0.0017, 0.0040]	0.4373
Prcp ² _{p1} (mm)	-4.20E-06	[-8.78E-06, 3.70E-07]	0.0716
Prcp ² _{p2} (mm)	-2.46E-05	[-3.32E-05, -1.61E-05]	<0.001
Prcp ² _{p3} (mm)	-1.01E-05	[-1.89E-05, -1.39E-06]	0.0230
P1 (day)	-0.0088	[-0.0131, -0.0045]	<0.001
P2 (day)	0.0293	[0.0132, 0.0454]	<0.001
P3 (day)	0.0093	[-0.0208, 0.0393]	0.5453
Observations	1,101		
R-squared	0.38		
AIC	2,813		
p-value (F-test)	<0.001		

Notes: Specific phenological periods: planting to double ridge (p1), double ridge to heading (p2), and heading to maturity (p3). Confidence intervals (CI) and p-values were estimated using clustered standard errors by location.

Table C.3. Coefficient estimates from modelling regression.

Variables	Coefficients	CI	p-values
Tm (°C)	0.1493	[0.0630, 0.2356]	<0.001
Tm ² (°C)	-0.0131	[-0.0177, -0.0084]	<0.001
Prcp (mm)	0.0057	[0.0039, 0.0075]	<0.001
Prcp ² (mm)	-5.37E-06	[-7.11E-06, -3.64E-06]	<0.001
Observations	1,101		
R-squared	0.35		
AIC	2,845		
p-value (F-test)	<0.001		

Notes: Confidence intervals (CI) and p-values were estimated using clustered standard errors by location.

Supplementary References

1. Sacks, W. J. & Kucharik, C. J. Crop management and phenology trends in the US Corn Belt: Impacts on yields, evapotranspiration and energy balance. *Agric. For. Meteorol.* **151**, 882-894 (2011).
2. Cesaraccio, C., Spano, D., Duce, P. & Snyder, R. L. An improved model for determining degree-day values from daily temperature data. *Int. J. Biometeorol.* **45**, 161-169 (2001).
3. Zhao, H. *et al.* US winter wheat yield loss attributed to compound hot-dry-windy events. *Nat. Commun.* **13**, 7233 (2022).
4. Zhu, P. *et al.* The critical benefits of snowpack insulation and snowmelt for winter wheat productivity. *Nat. Clim. Change* **12**, 485-490 (2022).
5. Zaveri, E. & B. Lobell, D. The role of irrigation in changing wheat yields and heat sensitivity in India. *Nat. Commun.* **10**, 4144 (2019).
6. Lobell, D. B., Schlenker, W. & Costa-Roberts, J. Climate trends and global crop production since 1980. *Science* **333**, 616-620 (2011).
7. Moore, F. C. & Lobell, D. B. The fingerprint of climate trends on European crop yields. *Proc. Natl. Acad. Sci. U.S.A.* **112**, 2670-2675 (2015).
8. Sacks, W. J., Deryng, D., Foley, J. A. & Ramankutty, N. Crop planting dates: an analysis of global patterns. *Global Ecol. Biogeogr.* **19**, 607-620 (2010).